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The determination of natural mortality and its causes in an exploited population of cockles (*Cardium edule* L.)

D. A. HANCOCK AND A. E. URQUHART

Fisheries Laboratory,
Burnham-on-Crouch

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CONTENTS

INTRODUCTION . . . . . *Page* 1

FENCED AREAS USED TO DETERMINE NATURAL MORTALITY . . 1
Methods 1
Results and Discussion 5

CAUSES OF NATURAL MORTALITY 7
Environmental conditions 8
Old age 8
Parasites and diseases 8
Predators 10
The common shore crab, *Carcinus maenas* (L.) . . . 11
The flounder, *Platichthys flesus* (L.) 12
The oystercatcher, *Haematopus ostralegus* (L.) . . . 15

NETTED AREAS TO PROVIDE ADDITIONAL INFORMATION ON OYSTERCATCHER DAMAGE 17
Method 17
Results from netted areas 19
Discussion of results from netted areas 20

SUMMARY AND CONCLUSIONS 21

ACKNOWLEDGEMENTS 22

REFERENCES 22

APPENDIX I Numbers of cockles of different ages from $\frac{1}{10}$ m² samples. Tables 2–6 24

APPENDIX II Instantaneous mortality coefficients and mean percentage losses of cockles 31

APPENDIX III Statistical examination of results. Tables 7 and 8 33

The determination of natural mortality and its causes in an exploited population of cockles (*Cardium edule* L.)

INTRODUCTION

THE observations described in this paper form part of a comprehensive study, undertaken at the request of the South Wales Sea Fisheries Committee, to investigate the causes of the recent decline in cockle landings from Llanrhidian Sands in the Burry Inlet, South Wales. The cockle beds cover a large area of the intertidal zone, and cockles are gathered by raking and sieving at low tide and transported by horse and cart.

The research programme included transect surveys to establish the extent of the main areas of fishable stocks and their total population; by repeating these surveys biannually, estimates have been obtained of the numbers lost from the fishery (i.e. *total mortality*) during winter and summer and throughout the whole year (Hancock and Urquhart, in prep.). An estimate of the number of cockles removed by fishing was also obtained from records of the number of fishermen and their catches throughout the year, kept by Mr K. J. Hutin, Fishery Officer to the Sea Fisheries Committee, whose assistance with all aspects of these surveys is gratefully acknowledged.

By comparing estimates of the total population in May 1959 and May 1960, the total mortality for the whole area during the year was estimated as 85%. The annual loss due to fishing during the same period was estimated as 14%. The difference between the two estimates is attributed to all causes except fishing, though it will include an element due to damage or loss as a result of fishing methods. These causes are grouped as *natural mortality*.

In most fisheries natural mortality can only be estimated as the difference between total mortality and fishing mortality. However, since cockles show negligible migratory movements and are completely accessible at low tide, separate estimates of natural mortality can be obtained. The purpose of this paper is to describe the principles and methods employed for determining natural mortality rates over a selected area of cockle bed on Llanrhidian Sands, and experimental work designed to separate the natural mortality estimate into its more important components.

FENCED AREAS USED TO DETERMINE NATURAL MORTALITY

POPULATION changes unaffected by fishing were examined by fencing off a series of small squares and taking samples regularly inside. Each fenced area was situated on one of the transect lines used in the population surveys, so that transect samples could also be used, together with extra samples taken near the outside of each fenced area, as controls representing an area where fishing was also in progress.

METHODS

To avoid hardship and possible temptation to cockle fishermen, while providing an area which would give adequate results, each area chosen to be fenced was small, with sides

10 metres in length. Early experiments showed that turbulence occurred round the base of each post as the tide passed, with a tendency to form a depression which remained filled by water during low tide (Plate 1). In order to reduce any adverse effects on the sampling area to a minimum, a one-metre border was allowed between the edge of the sampling area and the posts, i.e. each area was 12 metres square.

In early attempts at fencing an area on the cockle beds stout wooden stakes were used, their bases buried to a depth of $1\frac{1}{2}$–2 feet (= $\frac{1}{2}$ metre) in holes dug in the sand. These fences survived only a few weeks before strong tides washed them away. More success was obtained when strips of match boarding were nailed to the base of each post before it was buried, and some of these have survived for four years (Plate 1). More recently, however, a simpler technique has been adopted of hammering angle-iron stakes into the sand with a sledge hammer. The stakes were usually about $1\frac{1}{2}$ inches wide and were either obtained cheaply as dismantled bed-spring frames from a scrap dealer, or were conventional angle-iron fence posts. Each stake was 6 feet (2 metres) in length of which the bottom 2 feet were buried. Four or five stakes, including corner posts, formed each side of the square (i.e. 12 or 16 stakes per square), and the fence was completed by lashing or reeving P.V.C.-covered wire from post to post. It was helpful to have 2 holes drilled through each post so that the wire could be threaded through at 2 levels. The fence was intended to mark the area rather than to prevent entry, but the wires would help to prevent fishermen, bent forward while raking, from backing inadvertently into the sampling area. All fishermen and other interested persons were notified by a duplicated letter describing the experiment and asking them to co-operate by refraining from fishing inside the fenced areas.

The positions from which regular samples were taken are shown in Figure 1, which represents experimental work done on the selected area of the cockle bed known locally as 'First Arrow bed'. Each sample was $\frac{1}{10}$th square metre in area, marked off by a square of $1\frac{1}{2} \times 2\frac{1}{4}$ inch (38 × 56 mm) angled metal ('dexion') pressed into the sand, and the contents dug out with a spade to the depth, i.e. $2\frac{1}{4}$ inches, enclosed by the metal frame (Plate 2). No cockles were taken below this depth in either summer or winter. Each sample was sieved by water immersion (Plate 3) through a $\frac{1}{8}$-inch square-meshed brass sieve, and the contents placed in a jute bag (12 × 9 inches), the mouth of which was held open by a plastic plant-pot-holder from which the bottom had been removed (Plate 4). Each bag was tied with a waterproof label and contained a numbered plastic label. Later the cockles were separated from the shell and stones, sorted into year-classes and the numbers of each recorded. Each sample of sorted cockles, together with the plastic label, was then placed in a muslin bag and immersed in 5% formalin solution for about 24 hours. After subsequent rinsing in fresh water and careful drying, accumulated samples could be kept for many months for later measurement.

The area of each sample was limited to $\frac{1}{10}$th square metre, as this not only provided an adequate number of cockles but each sample just filled the sieve used for washing it, and the collection and sorting of samples of this size could be completed reasonably in the time available. Inside the fenced area (Figure 2) ten samples were taken to a pre-determined pattern and were expected to cover adequately any variations in density. Rough pre-selection of the sampling positions was expected to give a more reliable representation of the uneven distribution of cockles than taking entirely random samples, but their position may be considered to be random for all practical purposes because there was no visual selection, all the cockles being completely buried beneath the surface of the sand. The system adopted amounted to the sub-division of the area into sub-areas, with a random sample being taken from each. In this way there was little likelihood of samples taken at different times coming from an identical position, and this applied also to control lines and to transects. Outside the fenced area samples were taken, ten metres apart, five in an easterly and five in a westerly direction (Figure 1), and transect samples were separated by 50 paces (= *ca.* 38 metres) along a north-south line. Samples were taken every three months (Appendix I) so that population changes could be related to different seasons of the year. November was chosen as a convenient time in the cockle's life for commencing sampling, i.e. when cockles which had settled in early summer would be large enough for retention by sampling sieves, and when growth would have ceased for the winter.

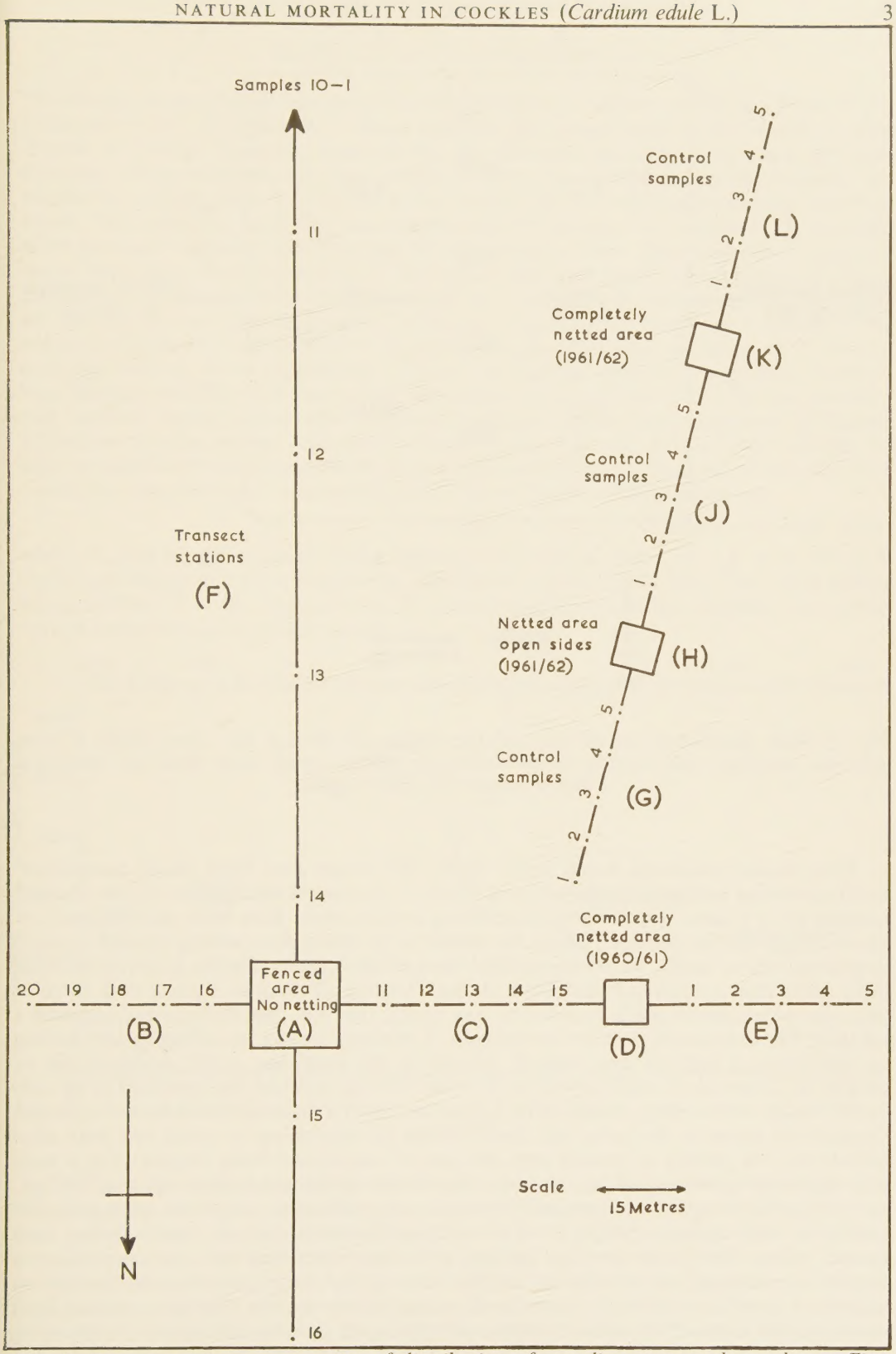


Fig. 1. *Diagrammatic representation of distribution of sampling areas and samples on First Arrow bed.*

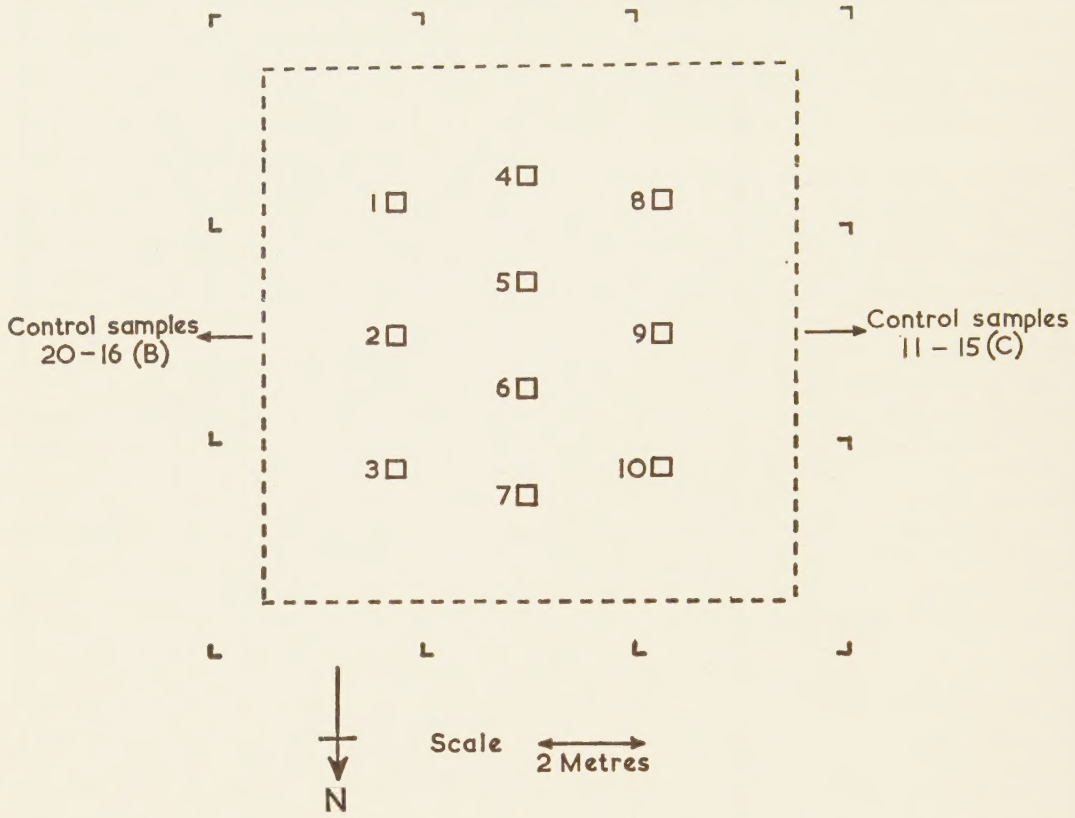


Fig. 2. *Scale diagram of fenced area (A) (see Figure 1). Broken line shows limits of area used for sampling. The positions of the angle-iron stakes outside these limits are indicated. Control samples 7½ metres apart.*

Only natural mortality would occur within the fenced area from which commercial cockle gathering had been prohibited (A in Figure 1). In control areas (B and C) and transect samples (F in Figure 1) the effects of gathering cockles could have been superimposed on the natural mortality pattern. Fishing for cockles is by raking and riddling through a sieve; in practice this is usually an oblong-meshed sieve which is more effective at letting through dead shells than a square-meshed sieve. A Sea Fisheries Committee Byelaw is in force in this area which prohibits the removal of 'any cockle that will pass through the gauge of a riddle or like instrument used for the purpose of riddling, sorting, or sifting cockles having an aperture of $\frac{3}{4}$ inch (19 mm) square'. A sieve of this mesh has a 50% retention size of cockles of 23 mm shell length. (Prior to 30 June 1959 the aperture was specified as $\frac{11}{16}$ inch or 17·5 mm, with a 50% retention of 21-mm cockles.) Undersized cockles are returned through the sieves to the beds, and these include all cockles up to about one year after settlement. The pattern of growth over the area of cockle bed being studied here is such that the faster-growing cockles enter the exploitable phase soon after one year of age, i.e. during July/August, but generally there is not a sufficient proportion of marketable cockles to make fishing worthwhile on this area until later in the year, that is during their second winter. Due to the very low survival of cockles older than two years the fishery is mainly concentrated on second-year cockles. During the winter months (mid-October to mid-May) growth ceases, and since not all second-winter cockles will have reached legal minimum size there will be selection within this group, till growth continues in the following summer. Virtually all cockles older than second winter would be retained by the sieve, but these are numerically few compared with younger cockles.

RESULTS AND DISCUSSION

The results obtained from sampling the selected areas are shown in Figures 3 and 4 and presented in full in Appendix I. When numbers per square metre were related to time (Figure 3) the first impression obtained was that for each year-class there was a very high mortality during both the first and second winters after settlement. As an example, the number of cockles which had settled in the summer of 1959 fell rapidly during their first winter, November to April; few were lost during the summer, but numbers fell from 906 to 54 between November and February of their second winter. This sequence of mortality might have been attributed merely to the adverse physical conditions experienced during each winter. However, a better understanding can be obtained by examining mortality *rates*, i.e. the loss per unit time expressed as a fraction or percentage of numbers present at the beginning of the time. According to accepted theories (Beverton and Holt, 1957) natural mortality behaves as an exponential function, so that the graphical relationship between logarithms of numbers and time should approximate to a straight line while the mortality rate remains constant, and any deviations should be immediately apparent. A further advantage of using natural logarithms is that the slope of their decline with time can be used to estimate the instantaneous total mortality coefficient (Z), from which the mortality during any time interval (t) can be estimated. This is based on the relationship:

$$N_t = N_0 e^{-Zt} \qquad \text{(Beverton and Holt, 1956)}$$

where N_0 and N_t are numbers at the beginning and end of time t. $Z = F + M$, where F and M are fishing and natural mortality coefficients, so that in the area from which fishing was prohibited $Z = M$. The value of M is thus equal to the slope obtained by plotting natural logarithms of numbers against time.

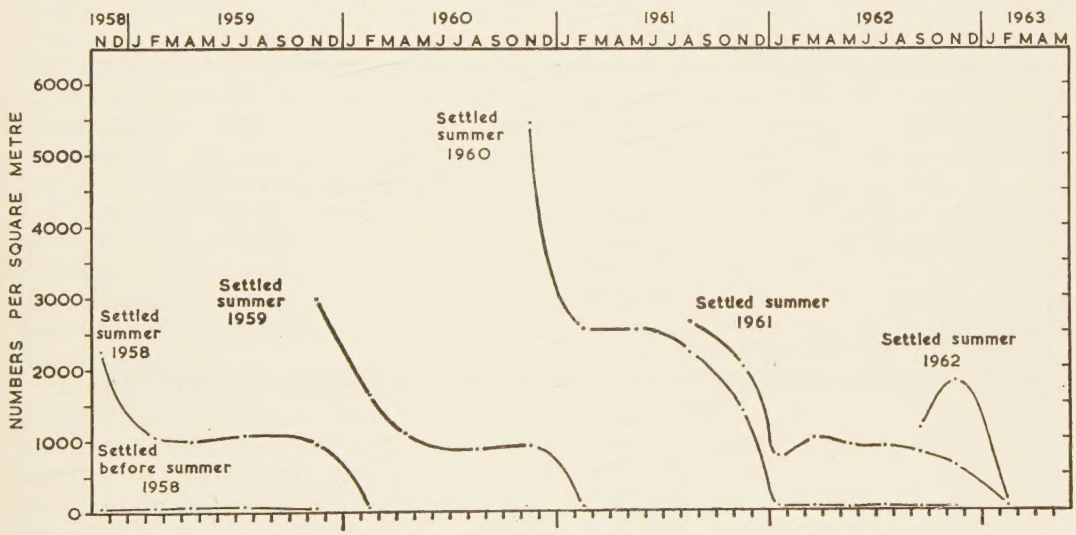

1958
1959
1960
1961
1962
1963
N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M
NUMBERS PER SQUARE METRE
6000
5000
4000
3000
2000
1000
0
Settled summer 1960
Settled summer 1959
Settled summer 1958
Settled summer 1961
Settled summer 1962
Settled before summer 1958

Fig. 3. *Changes in numbers per square metre of cockles which settled each year in fenced area (A).*

In Figure 4, natural logarithms of numbers per square metre have been related to sampling dates, each year-class being represented separately until the April/May following their second winter. By this time their numbers were too small to be useful and they were then grouped with the numbers of all other cockles a year or more older. The overall pattern of mortality suggested by the results from the fenced area, its controls and the transect was essentially the same. Taking as an example the 1958 year-class, its number declined at a fairly regular slow rate from November 1958 to November 1959. Between November 1959 and February 1960 there was a very heavy loss of these cockles, then in their second winter. Between February and April 1960 the rate of loss became much reduced,

and from April onwards the logarithms of the combined number of the 1958 and older year-classes followed a line with a slope more like that preceding the second winter. When the results from different year-classes were compared during the same winter, e.g. November 1959 to February 1960, it was evident that the exceptionally high rate of loss amongst

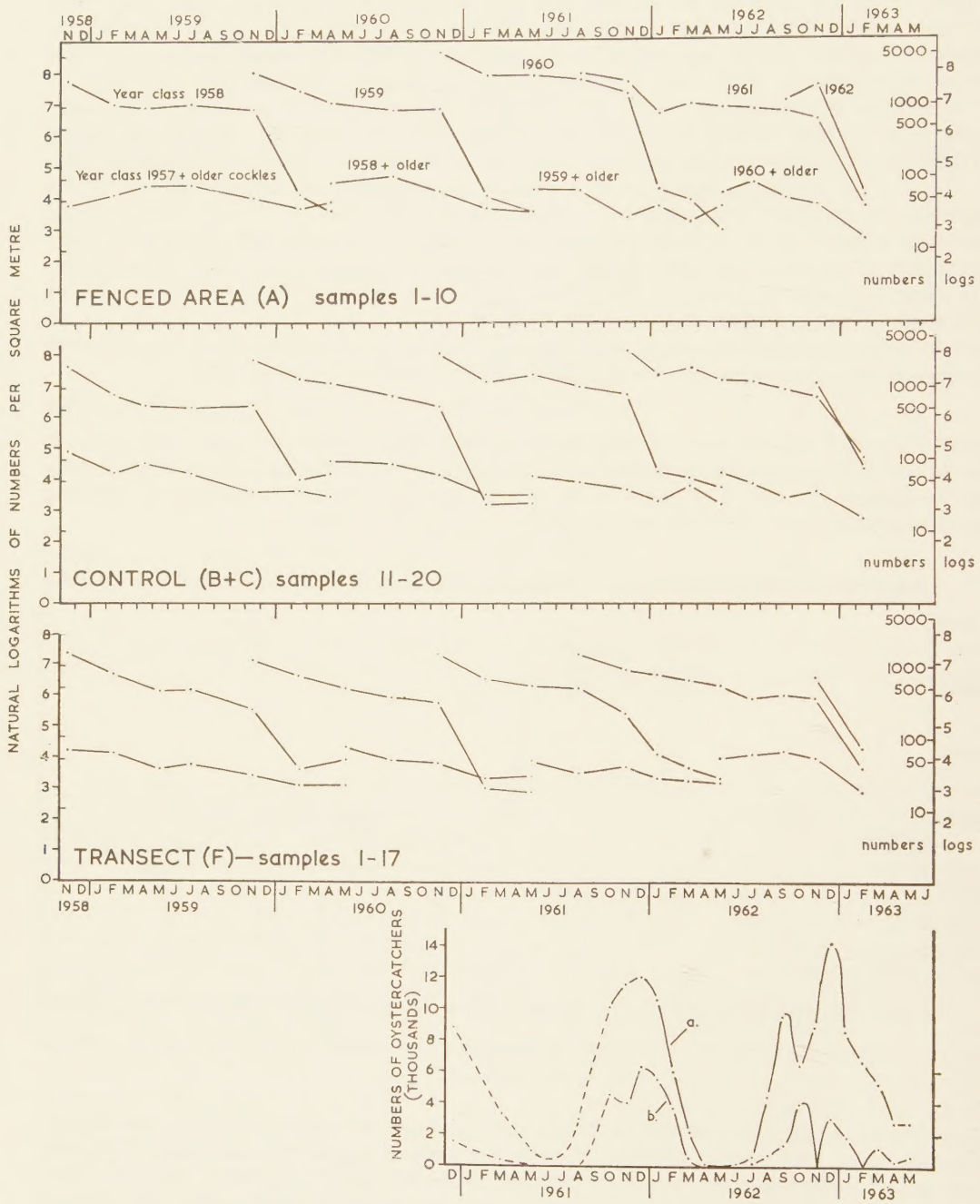

NATURAL LOGARITHMS OF NUMBERS PER SQUARE METRE
1958
1959
1960
1961
1962
1963
N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M
Year class 1958
1959
1960
1961
1962
Year class 1957 + older cockles
1958 + older
1959 + older
1960 + older
FENCED AREA (A) samples 1-10
CONTROL (B+C) samples 11-20
TRANSECT (F)— samples 1-17
numbers
logs
5000
1000
500
100
50
10
NUMBERS OF OYSTERCATCHERS (THOUSANDS)
a.
b.
D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M
1961
1962
1963

Fig. 4. *Changes in natural logarithms of numbers per square metre of cockles which settled each year on experimental areas on First Arrow bed. On the right-hand side the natural scale of numbers is compared with the logarithmic scale. The lower graph also shows numbers of oystercatchers counted at low tide by P. E. Davidson from* 1961–3*: (a) over the whole of Llanrhidian Sands, (b) First Arrow bed only.*

second-winter cockles (1958 year-class) did not occur amongst older (pre-1958), nor amongst younger (1959 year-class) cockles. The rate of loss of these cockles during their first winter was usually somewhat greater than during subsequent summer months, but it was nothing like as great as that of cockles a year older. The same sequence of mortality was observed for the 1959, 1960 and 1961 year-classes, i.e. the mortality rate of cockles increased very greatly during their second winter, over all three of the selected sampling areas. The winter of 1962–3 was, however, exceptional (Figures 4 and 6) but this was attributed to the effects of the unusually severe weather, during which first-winter cockles sustained a mortality equal to or greater than that of second-winter cockles, and the mortality of older cockles was also unusually high (Hancock and Urquhart, 1964).

The observed mortalities are now described numerically, but to simplify this account the methods used in calculating their values and their statistical significance are not included in the text but are presented in full in Appendices II and III. In Appendix II the results obtained from the three selected sampling sites have been compared and averaged over the years 1958–62. The figure obtained for the average loss of cockles during the three months November to February following settlement was 48%, compared with an average of 21% per three months for the three subsequent three-monthly periods up to the November commencing the second winter. During the whole year from the November after settlement to the following November the average three-monthly loss was 29%, giving the quite substantial annual mortality of 74%. This figure contained results from unfenced areas in which there may have been some loss due to fishing during the second summer; inside the fenced area alone the comparative percentage loss was lower, being 25% per three months and 69% for the year.

Lamellibranchs generally sustain heavy losses during the year or so after settlement, and the cockle would not be expected to be an exception, especially in view of its dependence for survival on retaining a position in the surface layers of a relatively unstable environment subjected to extremes of both air and water temperatures. The higher rate of loss (48%) during the first three winter months of the period examined could have resulted in part from unfavourable winter conditions, and therefore, apart from a slight increase resulting from similar causes during the second winter, the annual mortality rate might be expected not to increase after the first year until affected by factors associated with old age. The great increase in mean mortality rate to 92% of second-winter cockles between November and February was therefore unexpected, particularly since it was followed during subsequent months by the comparatively low average mortality rate of 19% and later of 13% per 3 months, or 57% and 43% respectively per annum. For comparison, the average annual loss of cockles older than second winter estimated from transects covering the whole of Llanrhidian Sands for the years 1958–62 was 63%, but this figure certainly included losses due to fishing.

In view of the fact that the high second-winter mortality occurred both outside and inside the fenced area it could be suggested that it resulted from fishing. However, a good proportion of second-winter cockles are not retained by the sieves used, which means that fishing would have resulted in an even greater loss of older cockles, almost all of which were large enough to be fished legally, but this was not so. In any case there was nothing to suggest that poaching had occurred inside this fenced area; in other experiments (to be described in a later paper), when poaching from another fenced area occurred at a time of extreme shortage of cockles this was clearly indicated by the results of sampling. The losses observed must therefore have resulted from one of the causes examined in the next section.

CAUSES OF NATURAL MORTALITY

In an area subjected to fishing, when natural mortality is estimated as the difference between total mortality and numbers removed by fishing, the estimate will also include an element of loss due to damage resulting from human activities. Undersized cockles passing through the sieves may have been damaged by raking and sieving, and some of these sieved cockles

left exposed on the surface may be lost as a result of disturbance by the incoming tide. The passage of men, horses and carts across the beds will also cause damage. None of these effects would however occur inside the fenced area, and in any case experiments have shown that losses from damage and disturbance are generally greatest amongst the smallest cockles.

Causes of losses of cockles other than those connected with fishing include:

Environmental conditions
Old age
Parasites and diseases
Predators

These causes are now examined to decide on the contribution each was likely to have made to the mortalities observed.

ENVIRONMENTAL CONDITIONS

Deaths due to adverse environmental conditions, including wave action and low temperatures, are generally greatest amongst the younger cockles. Large numbers of first-winter cockles were occasionally observed accumulated at high-water mark or floating at the edge of the tide, notably in April 1960 and February 1962. In the Burry Inlet and elsewhere, extreme winter conditions such as occurred in January 1963 were found to affect second-winter cockles least (Hancock and Urquhart, 1964), and an exceptionally heavy loss of first-winter cockles was recorded on First Arrow bed in the winter of 1962–3 (Figures 4 and 6). Kristensen (1957) found that decreases in the density of the population resulting from washing out and transport to unfavourable conditions were most likely to occur during the winter months, when the speed of digging-in is reduced. This effect was said to be most pronounced amongst cockles of less than 2 mm shell length, which cannot dig deeply enough, and cockles aged 3 years and older, in which the digging-in speed becomes slower.

In early summer moribund cockles are frequently seen on the surface of the sand, and in May 1959 their numbers over a small area were compared with the numbers of live cockles in the adjacent sand. Dead one-year-old cockles were few, while moribund cockles older than two years were predominant. It is possible that this was associated with some post-spawning effect on older cockles. Orton (1933) similarly found large numbers of cockles containing dead flesh on the surface in Morecambe Bay in May 1933, and concluded that the mortality, amounting to some 5% of the population, was associated with the effects of warm summer conditions on post-spawning cockles. Kristensen (1957) suggested that similar losses in early spring 1948 and in May 1949 may have been due to parasites.

None of these effects of adverse environmental conditions, however, appear to explain the heavy losses of second-winter cockles. It should also be remembered that in the winter of 1961–2 (Figure 4) the greatest loss of second-winter cockles occurred between November and January, and was greatly reduced from January to March, a period which undoubtedly included bad weather conditions.

OLD AGE

Losses due to old age do not assume any great importance in this fishery because, although the lifespan of the cockle can exceed 10 years in this area, mortalities of the magnitude observed during the second winter of life, coupled with selective fishing of the older cockles, allow only very low survival of cockles older than 4–5 years in the fishery. For example the results of a survey in May 1962 showed that only 3% of cockles rising two years and older exceeded five years of age. The proportion of total stocks lost as a direct result of old age is therefore very small.

PARASITES AND DISEASES

Cole (1956) recorded many parasites and commensals from *Cardium edule*, including ciliates, trematodes, turbellarians and copepods.

During the course of routine examination of live smears from the gonads of cockles from Llanrhidian Sands throughout the year, any parasites observed were recorded but usually no special search was made for them. The sporocyst stage of *Bucephalus haimeanus* Lacaze-Duthiers, however, infests the gonad and digestive gland and often seriously damages or destroys the gonad (Cole, 1956); particular attention was therefore given to this species. Cole found that 2% of cockles from North Wales were infested by the sporocyst stage of this trematode parasite. In the present samples, sporocysts containing cercariae with characteristic paired tail processes at all stages of development were easily recognizable in gonad smears (see Lebour 1912, and similar to *B. mytili* figured by Cole 1935). The characteristically reticulated appearance of the foot of the cockle, caused by numerous thread-like sporocysts beneath its surface, also allowed macroscopic recognition. No sporocysts were found in cockles less than one year old, though many were examined. The results obtained from cockles older than one year were as follows:

	Second-year cockles			*Older cockles*			
	Number examined	*Number infected*	*% infected*	*Number examined*	*Number infected*	*% infected*	*Mean %*
May 1959–May 1960	123	19	15	108	8	7	12
May 1960–May 1961	66	1	2	83	3	4	3
May 1961–May 1962	38	0	0	50	9	18	12
TOTAL	227	20	9	241	20	6	8

From these limited records it appears that the average infection for cockles of all ages greater than one year was 8%, but the annual figure showed marked variation between different ages and from year to year. *Bucephalus* were observed during most months of the year, and the highest infection rate recorded on one occasion was 38% (3 out of 8) amongst older cockles in July 1961 and amongst second-year cockles 40% (2 out of only 5 examined) in February 1960, and 22% (8 out of 36) in April 1960. In 37 out of the total of 40 infested cockles no traces of sex products were seen. The remaining three contained either eggs or sperm in addition to sporocysts. It is not known what other harmful effects these parasites have on cockles, apart from causing parasitic castration. Menzel and Hopkins (1955) consider that *Bucephalus cuculus* have a beneficial effect on American oysters from a gastronomic standpoint, because the castrated oysters remain fat and tasty while those without infection lose flavour and condition as a result of spawning. However, they concluded from their rather limited observations and those of other authors, that while the parasite is confined to the gonad growth may be improved, but its invasion to other tissues would adversely affect normal functions. One mussel from Conway, infected with *B. mytili* Cole, was found to have a meat volume less than average for normal mussels of the same shell length (Hancock, 1962), but no observations like this were made on cockles. However, none of the extreme wasting conditions caused by 'orange sickness' (*Cercaria tenuans*) of mussels (Cole, 1935) were observed. It is not known whether a *Bucephalus* infection normally causes the death of the host, but it is agreed with Cole (1956) that this is unlikely, from theoretical considerations. On the other hand Millar (1963) found that when oysters infected by a Bucephalid were kept in laboratory tanks most of them died.

The other trematode parasites recorded by Cole (1956) were not seen in cockles from Llanrhidian Sands but no special search was made for them. However, E. Bowers (pers. com.) of University College, Swansea recorded 100% infection by what he calls metacercaria (*Gymnophalloides oedemiae*) (Jameson and Nicoll, 1913; James, 1964) from under the hinges of cockles exceeding 17 mm shell length, i.e. during their second year, from Llanrhidian Sands. This species was referred to as *Cercaria cambrensis* Cole by Cole (1956), who found 100% infection by the sporocyst stage on North Wales cockle beds.

The following animals were also observed incidentally to investigations of gonads from Llanrhidian Sands cockles:

Parenthessius rostratus Canu was recorded by Cole (1956) as common in the mantle cavity of cockles, and this copepod was seen frequently in the shell water of cockles of all ages from Llanrhidian Sands, even from some only 6 months old. A careful examination showed its presence in ten out of twelve older cockles.

Trichodina cardii (Delphy), a peritrichous ciliate recorded by Cole as common in the mantle cavity of cockles from North Wales, also occurred frequently on Llanrhidian Sands. Even though usually no special search was made for *Trichodina* its presence was noted in 12% of 438 cockles of all ages examined. It was observed at all seasons of the year and in all ages of cockles, including four out of five cockles examined at 6 months of age. A 13-mm cockle nearly a year old contained at least 4 individuals.

Paravortex cardii Hallez, a rhabdocoel turbellarian recorded by Cole (1956) as common in the gut, was also observed in all ages of cockles from Llanrhidian Sands, and even without a special search 13% of 428 cockles examined on various occasions were seen to contain this parasite. A careful search revealed the presence of *Paravortex* in eight out of ten 15-mm cockles nearly one year old. The parasites were present throughout the year, and young individuals and adults containing young were observed in October 1960, January 1961 and August 1961.

There is no evidence that parasitization causes the early death of cockles, and even if it did it would not explain the different mortality rates observed between age groups.

PREDATORS

The factors so far mentioned, although contributing to the general level of mortality on Llanrhidian Sands, provide no evidence as to the cause of the heavy loss of second-winter cockles. A remaining possibility is that of predation, and the occurrence of heavy losses amongst one age group is suggestive of a predator feeding selectively on second-winter cockles. Beverton and Holt (1957, p. 68) state that a discontinuity would arise in the trend of natural mortality rate with age, where predation is sharply restricted to individuals of a certain size range. (The same authors suggest that an increase of natural mortality rate with age may also commence at the age of first maturity as a result of the drain of spawning. Cockles generally produce a small amount of spawn about one year after settlement, and development of their first major production of sex products occurs during their second winter, for liberation during the following spring. However, it is thought unlikely that the onset of maturity is a relevant factor connected with the high natural mortality of second-winter cockles on Llanrhidian Sands, a mortality which is not known to occur on cockle beds elsewhere and which does not persist in older cockles.) Known predators of cockles, other than man, include certain invertebrates (boring snails, starfish and shore crabs), fish and birds. On Llanrhidian Sands the only invertebrate predators recorded were shore crabs (*Carcinus*), and these were seen in only small numbers. Fish, mainly flatfish such as flounders, occur in quite large numbers and constitute a fairly profitable stake-net fishery on Llanrhidian Sands when they move into the intertidal zone while the tide is in. Large numbers of birds frequent the cockle beds on Llanrhidian Sands at low tide; these include oystercatchers, gull species, knot, dunlin, curlew, carrion crow, shelduck, etc. The most numerous species is the oystercatcher (*Haematopus ostralegus* L.), which has already been recorded as an important predator of cockles in other areas in Britain by Drinnan (1957), while Kreger (1940) and Kristensen (1957) list oystercatchers amongst the causes of winter mortalities on Dutch cockle beds. Herring gulls are said to eat cockles (Kreger, 1940), but on Llanrhidian Sands they have been observed to eat only cockles which were exposed, broken or gaping on the surface, including those damaged by fishing or by the progression of horses and carts across the beds (Plate 5). Little is known about the food of the other bird species, there being no observations on their feeding on cockles on Llanrhidian Sands.

THE COMMON SHORE CRAB, *Carcinus maenas* (L.)

Orton (1926) concluded from his field experiments on the growth of *Cardium* that the shore crab is a great enemy of small cockles. On the cockle beds of Shoeburyness, Essex, where the occurrence of crabs in the intertidal zone during the high-tide period could be investigated readily by trawling and dredging, up to 84 adult crabs were taken during the summer of 1959 in a 30-minute haul with a 12-ft beam trawl, and up to 13 crabs per 5-minute haul with a 2 ft 6 inch hand dredge. On Llanrhidian Sands, however, access by boat at high-water time is difficult due to the presence of many posts and beacons in the intertidal zone which make trawling or dredging impracticable. In this area information on crab numbers could only be obtained from the results of transect samples and from whelk pots baited with fish and left on the cockle beds overnight. The numbers of crabs per square metre, estimated from samples dug at low tide from Transect (F) and fenced area (A) (Figure 1), are shown in the following table:

Date	*Transect (F)*	*Fenced area (A)*
Nov. 1958	2	1
Feb. 1959	1	1
Apr. 1959	0	2
July 1959	6	11
Nov. 1959	4	5
May 1960	2	Not taken
Nov. 1960	2	0
May 1961	0	0
Aug. 1961	1	10
May 1962	4	2
July 1962	1	1

None of the crabs recorded here exceeded 30 mm carapace width, and the majority were extremely small, with carapace widths of about 10 mm. According to Naylor (1962) small crabs of less than 30–35 mm carapace width were present at low tide on the shore at Swansea throughout the year, and they seemed to move about much less than larger specimens. No adult crabs were found stranded by the tide in the area covered by Transect (F), a flat area of sandy mud with little or no cover, though on one occasion (April 1960) several large *Carcinus* (*ca.* 50 mm) were taken buried in the sand on another part of the cockle bed.

The results obtained from whelk pots were:

Date	*Number of pots*	*Bait*	*Time left down*	*Number of crabs caught*
May 1960	3	Fresh flatfish offal	24 hours	19
	3	Fresh flatfish offal	72 hours	2 + 4 small
	3	Fresh whiting	24 hours	2
	3	Fresh whiting	24 hours	6
Aug. 1961	5	Salted skate	24 hours	2
Feb. 1962	2	Salted skate	24 hours	0
	2	Salted skate	24 hours	0

It must be remembered that the capture of crabs in baited pots only gives a guide as to whether they are responding to the food offered at that time. These crabs measured about 30–55 mm carapace width.

Naylor (1962) used similar whelk pots baited with fish, but also collected crabs by hand at low tide amongst rocks on the foreshore at Swansea. He concluded that crabs larger than 35 mm carapace width migrate upshore on each high tide and back again with the ebb, but in summer many were left stranded beneath stones at low tide. In December and March they still migrated upshore but few were left stranded, while in January and February upshore migration ceased.

B. W. Jones (pers. com.) in laboratory experiments found that adult crabs (50–70 mm carapace width) fed actively on small cockles kept in tanks without sand at temperatures above 6°C, while below this temperature feeding virtually ceased. It is significant, however, that crabs have been caught in baited pots in the River Crouch during the winter months at a temperature of 4°C. In Jones' experiments up to 39 first-winter cockles (shell length *ca.* 15 mm) were eaten per crab per day. There was a tendency for the smallest cockles in the range 10–22 mm to be eaten, and for fewer cockles to be eaten when buried in the sand than when exposed. In similar laboratory experiments by the present authors, adult crabs ate up to 36 first-winter cockles each per day during April. In July crabs ate one-year-old cockles in the range 17–20 mm at roughly 3 each per day by breaking the shells, and in August cockles as large as 22–27 mm (all just older than one year) were eaten at about the same rate.

In November 1963, crabs were collected (from transect samples) in the range 4–17 mm carapace width, and when placed in tanks they had no difficulty in breaking open the shells of small first-winter cockles.

More observations are required on the feeding of *Carcinus* on *Cardium*, but in relation to the Llanrhidian Sands problem it may be concluded that:

1. Adult *Carcinus*, i.e. larger than 35 mm, are most likely to move onto the shore during the summer months, but they are unlikely to remain there at low tide, due to lack of cover.
2. There is no quantitative information on the numbers of adult crabs moving onto the shore, but the indications are that they are few, and generally only a few small crabs occurred in transect samples.
3. In captivity, crabs of 50 mm and larger are capable of eating the whole size range of cockles up to 2 years of age, but it is not known to what extent this occurs in nature.
4. The evidence available suggests that although *Carcinus* may have contributed to summer mortality to a small degree they cannot have caused the heavy mortality of second-winter cockles observed during each winter.

THE FLOUNDER, *Platichthys flesus* (L.)

Recent observations from a number of localities in Britain have shown that various species of fish, particularly flatfish, include cockles in their diet. Fish move towards the shore at high tide, as demonstrated by the landings from intertidal stake-net or stop-net fisheries, of which there is a good example on Llanrhidian Sands. It has not been possible to make a quantitative assessment of this fishery, but several nets are worked regularly, mainly between August and November, with good results, fishing mainly on a falling tide, i.e. between spring and neap tides. At present best catches amount to about 150 fish per net of about 200 yards length, and these are almost all flounders with only occasional plaice, soles, turbot, bass and mullet. There are at present only about 4 fishermen, compared with 23 in the 1920's, and the quantity of fish caught per net now is also said to be less.

There are many published observations on the food of the flounder (e.g. Herdman and Scott, 1895; Ascroft, 1900; Murie, 1903; Blegvad, 1932; Larsen, 1936; Hartley, 1940; Williams, Perkins and Hinde, 1963). Of these Ascroft, Murie and Hartley concluded that crustacea and annelids were the most commonly taken food, but molluscs were also eaten. Herdman and Scott concluded that in 1894 the chief food of flounders included annelids, crustacea and molluscs (in that order of importance), compared with molluscs, annelids and crustacea in the previous year. Blegvad however found that in the Baltic the dominant food changed from crustacea (O-group fish) to crustacea and chaetopoda (I-group) to molluscs (II-group), and Larson found that the most commonly eaten foods in the Dybsø Fjord were *Cardium exiguum*, *C. edule*, *Idotea* and *Gammarus*. Williams *et al.* (1963) showed that the main food of flounders in the Solway Firth is composed of lamellibranchs, with *Mytilus*, *Cardium* and *Macoma* (in order of importance) in the inner area and *Cardium*, *Macoma* and *Abra* in the outer area. Crustacea, including *Corophium* and *Crangon*, were also eaten. In one of their samples in June 1962 (Perkins, pers. com.), 27 flounders of length

25–35 mm contained 751 *Macoma*, 543 *Cardium* (all under 18 mm long) and 9 *Hydrobia*. He also concluded that in the Solway area plaice, with 36% of their diet composed of cockles, were more important as predators than flounders, in which cockles comprised 18% of the total food taken. Kristensen (1957) concluded that on the intertidal flats of the Dutch Wadden Sea the flounder had no significance as a consumer of cockles but he had few observations. Hartley (1940) listed 39 separate items of food for flounders, and concluded that the choice of food eaten was influenced by the age of the fish and the food most readily available. He found that immature flounders fast during the winter months, while mature fish continue to feed for a while before fasting, though most of the pre-spawning fish left the Tamar and Lynher estuaries in January for spawning offshore in the early spring. Williams *et al.* also found fewer fish during the winter months, and the amount of food eaten by these was greatly reduced compared with that in the summer months. Herdman and Corbin (1894) found that flounders leave the rivers and estuaries in which they usually occur and move offshore during the winter, in preparation for spawning in March. These observations support the claims of Llanrhidian Sands fishermen that fishing is uneconomic during the winter months.

The present investigation was confined to the examination of gut contents of flounders taken in stop-nets on Llanrhidian Sands during the normal fishing season. In addition, a professional fisherman was persuaded to erect his nets during February 1962 near to our experimental area of First Arrow bed, which is a quite cominonly used site for stop-netting. This was during a normal winter, unlike the following severe one, but as forecast by the fisherman the catches were very poor, consisting of only 11 flounders from five daily inspections (maximum of four fish in one day) and insignificant catches in several subsequent weeks. This may be compared with a single day's catch of 38 flounders in November 1962 at the end of a poor year, and higher catches during the summer months.

A summary of the results obtained from flounder guts is given in Table 1. In addition, flounders examined from the Thames Estuary, Conway and Morecambe Bay were also found to contain small cockles, which were readily identifiable throughout the gut from shell fragments which remain undigested, and from which the numbers of hinge ligaments could be counted. In the four samples taken during different years in August, September, October and November from Llanrhidian Sands (Table 1) nearly all of the fish contained cockles, and in all except the November sample cockles were the most important food. In these samples large numbers of cockles (up to 290 per flounder) were found to have been eaten, and all of these were brood cockles (O-group) settled only a few months previously. In February, very few cockles were found and some of the fragments appeared to be from cockles in their second year. In June and July samples again few cockles were found, and some of these were small individuals entering their second year. It seems that cockles younger than one year old are the most likely to be eaten, but when they are in short supply, occasional small older cockles are taken. On the occasions when cockles older than one year were taken their numbers were few and they were by no means the most important food in the gut.

Table 1 shows that large quantities of food other than cockles were taken, principally *Corophium* and other amphipods (probably *Bathyporeia*). Individual fish often showed a marked preference for a particular food, e.g. in November 1962 one flounder contained about 1,600 *Corophium* with just a few *Hydrobia*. In the same sample another fish contained 74 *Cardium* with little else, and in August 1961 a fish contained 290 *Cardium* with a few *Hydrobia*. However, in this sample there was also a fish which contained the largest number of *Macoma* (135) but had eaten also 45 *Cardium*, 22 *Hydrobia* and a few amphipods, while a flounder which contained no lamellibranchs had eaten nearly 600 amphipods as well as 142 *Hydrobia*, some worm fragments and several other crustacea. The diet may include a mixture of crustacea and molluscs, while in some cases a succession of foods may be present, as in a fish in November of which the rectum and stomach were full of *Corophium*, while the intestine in between contained only cockles.

It may be concluded that each flounder moving into the intertidal zone is a potential predator of cockles, capable of eating on average about 120, almost entirely brood, per high-water period, at least during the 3 months August to October. A more precise estimate

Table 1. *Analysis of gut contents of flounders caught in stop-nets on Llanrhidian Sands*

Date	No. of fish examined	Length of fish (mm)		Mean volume of food (ml)	% of fish with empty guts	% of fish containing cockles	% of fish in which cockles were the most important food	Numbers of cockles per fish		Cockles eaten*		Species eaten, roughly in order of numerical importance
		Range	Mean					Range	Mean	Approx. Age (months)	Shell Length (mm)	
June 1960	6	280–310	300	Fairly full	0	100	0	5–65	21	mainly 2 (some 14)	mainly 2 (some >12)	*Corophium, Hydrobia, Macoma, Cardium*
August 1961	42	175–360	300	13·8	0	100	79	8–290	116	4	2–12	*Cardium, Macoma,* amphipods†, *Corophium, Hydrobia, Carcinus, Arenicola,* Isopods‡
October 1961	17	250–363	307	Fairly full	0	94	94	0–230	127	6	4–11	*Cardium, Hydrobia, Macoma,* amphipods, *Scrobicularia, Carcinus*
February 1962	11	190–330	258	Not very full	9	45	0	1–2	0·5	10 and 22	3–5	amphipods, *Hydrobia, Corophium, Cardium, Carcinus, Macoma,* Isopods, annelids
July 1962	33	226–385	294	3·7	9	48	30	0–22	4	3 and 15	2–4 and >12	amphipods, *Cardium, Macoma,* Isopods, *Crangon, Hydrobia, Corophium,* annelids
September 1962	15	248–368	314	12·2	7	93	73	0–244	106	5	6–13	*Cardium, Corophium, Hydrobia, Macoma, Carcinus, Crangon*
November 1962	38	189–377	249	6·2	0	84	47	0–74	23	7	5–14	*Corophium, Cardium, Hydrobia, Macoma, Carcinus, Crangon,* annelids

* Only a small proportion of cockles eaten were measurable.
† probably *Bathyporeia.*
‡ probably *Sphaeroma.*

of the daily intake, i.e. during 2 tides, is not possible without information on the rate of passage of food through the gut, and diurnal variation of food intake. Williams and Perkins (pers. com.) believe that as a general rule flatfish in the Solway Firth are unable to obtain sufficient food below low-water mark and will therefore move towards the shore and feed at whatever time of day or night the high-water period occurs. Their samples were, however, mainly taken after dawn, and flounders were most often full when low water occurred near the time of dawn. Llanrhidian Sands fishermen consider that catches are best when nets are examined after a high-tide period during the night.

As a very rough estimate a flounder may on average consume 120 brood cockles per tide during say 100 days – *ca.* 12,000 cockles, or (if the feeding rate is considered to be similar during both high tides each day) twice this quantity, i.e. 24,000. Stock estimates suggest that the average number of brood cockles present on Llanrhidian Sands each August is of the order of 4,000 millions. The average loss of brood cockles between August and November is estimated to be 1,000 millions. A daily population of *ca.* 40,000 flounders feeding at an average rate of 120 cockles per tide, two tides a day for 100 days would be needed to consume 1,000 millions, but this figure also includes cockles lost from a variety of causes in addition to predation.

Flounders on Llanrhidian Sands thus constitute a source of predation of brood cockles during the summer months. However, during the winter their feeding activity in the intertidal zone becomes reduced as a result of lowered food intake and offshore migration. Flounders cannot, therefore, be held to be responsible for the heavy losses of second-winter cockles during each winter. A measure of control is already applied indirectly by fishing them for human consumption.

THE OYSTERCATCHER, *Haematopus ostralegus* (L.)

A full account of observations on oystercatchers in the Burry Estuary is being prepared by Mr P. E. Davidson of the Fisheries Experiment Station, Conway. The inclusion of the following notes here is considered desirable to enable the reader to judge the validity of the conclusions reached in this account.

Presence of oystercatchers on the cockle beds

Large flocks of oystercatchers have been recorded feeding on Llanrhidian Sands cockle beds each winter for a number of years. In winter 1955–6 the damage they caused was reported by the Fishery Officer, Mr K. J. Hutin, and in 1956–7, 2,150 birds were recorded in a single count during the winter (Drinnan and Cole, 1957). During a series of counts throughout each year, commencing in December 1960, Davidson recorded a maximum number of 8,837 oystercatchers feeding on the cockle beds in December 1960, 11,966 in December 1961, and 14,100 in December 1962, and confirmed that most of the birds arrive in October with numbers increasing to a maximum in December. The flocks have begun to thin out by mid-February and by early summer only a small flock of mostly immature birds remains. These observations confirm Drinnan's (1957) conclusion that oystercatchers have a winter feeding cycle on British cockle beds, the main flocks of mature birds migrating north to breed during the summer months. Figure 4 shows the numbers Davidson recorded in counts between December 1960 and May 1963 over the whole cockle bed, and it can be seen that peak numbers coincided with the time of maximum disappearance of cockles during their second winter. The numbers actually feeding on First Arrow bed during the monthly counts are also shown in Figure 4.

Evidence of feeding

Evidence of feeding by oystercatchers was provided by direct observations on birds removing cockles from the sand after probing with their beaks, and Davidson will report his extensive observations on the distribution of feeding birds over Llanrhidian Sands, their

feeding behaviour and rates of feeding. Each winter, large areas are covered by characteristic heaps of broken shells (Plates 6 and 7), and this habit of carrying the cockles to a selected patch before opening them was described by Drinnan (1957). The shells were broken in a manner characteristic of feeding by oystercatchers (Drinnan, 1957 and Plate 8) and often contained traces of flesh. The number of shells in a heap, each measuring several feet across, was formidable (Plate 7). During the course of surveys of First Arrow bed, feeding oystercatchers or their shell heaps were seen by the authors in February and November 1960, February and December 1961, January, February and November 1962, in addition to Davidson's observations.

Selection of second-winter cockles

The examination of feeding heaps during each winter showed that they were regularly composed almost entirely of second-winter cockles. Typical examples of shell samples from feeding heaps have been compared with the age composition of cockles living in the sand nearby as follows:

	% at each age among:					
	Dead shells from heap			Live cockles from sand		
	First-winter	Second-winter	Older	First-winter	Second-winter	Older
Sample 1	1	89	10	50	18	32
Sample 2	6	92	2	96	3	1

It appears that there is a definite selection of second-winter cockles from areas containing many first-winter cockles, as shown by the beak probe marks in Plate 9. However, on some occasions first-winter cockles may be eaten in quantity, but usually only when older cockles are in short supply, such as at the end of the winter. For example, oystercatchers were observed to eat cockles just less than one year old in May of each year, but the empty shells usually remained in the beak holes and were not concentrated into heaps. This was again observed in November 1963, when cockles older than this were unusually scarce as a result of the previous severe winter. Cockles older than second winter are normally numerically the smallest age group, but the figures tabulated above show how they seem not to be preferred, though again in unusual circumstances such as the poor stocks of particularly second-winter cockles in November 1963, cockles older than second winter were eaten as well as first-winter cockles. On other occasions, such as January and March 1962, one area was found to carry numbers of empty shells of cockles older than second winter spread over the sand. These shells were chipped at the posterior end and they were believed to have been opened *in situ* by oystercatchers probing at the siphons while the cockles remained covered with water during the falling tide. This behaviour occurred at a time when the numbers of second-winter cockles had been reduced to less than those of older cockles, but despite this, shells broken during low-water feeding and concentrated into heaps on the same area were predominantly of second-winter cockles. Live older cockles were sometimes found amongst the broken shells in feeding heaps, as in the following example, which shows how second-winter cockles had been selectively killed even though the numbers of older cockles living in the sand now exceeded those of second-winter cockles. Only a few broken shells of older cockles were present, though some live ones had been concentrated on the surface among the broken shells:

January 1962		*Numbers of cockles* First-winter	Second-winter	Older
In sample from feeding heap	Dead	0	71	3
	Live	2	4	9
Living in sand (per m²)		6070	29	40

It was concluded that the greatest mortality due to oystercatchers occurs amongst second-winter cockles, though those older and younger will both also suffer some losses.

This conclusion supports the view that the heavy losses observed amongst second-winter cockles on First Arrow bed resulted largely from oystercatcher predation. In addition, oystercatchers were seen on many occasions to be feeding both inside and outside fenced areas (Plate 10). In order to obtain more direct evidence on the amount of predation by oystercatchers, it was decided to exclude them from an area by covering it with wire netting, and to compare the changes in cockle numbers under the netting with those outside where oystercatchers had not been prevented from feeding.

NETTED AREAS TO PROVIDE ADDITIONAL INFORMATION ON OYSTERCATCHER DAMAGE

METHOD

In November 1960 a site was chosen near the fenced area on First Arrow bed (Figure 1, D). A smaller plot was used because of the need for keeping the wire netting well off the ground (a) to prevent the birds from putting their beaks through the meshes and (b) so that the wire would interfere as little as possible with the natural condition of the surface of the bed. The construction of a typical netted area is shown in Figure 5 and Plate 11. The sampling area covered 25 square metres, but a border of $\frac{1}{2}$ metre was allowed all round (i.e. 6 metre sides) before erecting the angle-iron corner posts. One or two intermediate posts were used for each side, together with a single post in the centre of the area to keep the wire netting raised off the sand. It is desirable to keep the number of stakes, particularly in the centre, to a minimum to reduce any effects of tidal washing round the bases of the stakes. Only about 36 inches of each five feet long perimeter stake was left remaining above the ground. P.V.C.-covered wire as used in existing fences was lashed to a perimeter stake (or rove through a hole) 12 inches above the ground, hauled taut and lashed to the centre stake a few inches from its top. The wire was then passed on to the stake opposite, tightened and made fast 12 inches above the ground. This procedure was repeated for each pair of opposite stakes. If there was a tendency to slackness in the radii they were tightened by lashing an extra wire between them. Lengths of 2-inch mesh chicken wire had been previously cut and joined to the correct size and the centre marked by a label. This was lifted into position over the centre stake, squared up, hauled tight and fastened by passing a convenient mesh over a perimeter stake. Two lengths of wire were woven along each side, one at ground level through the edge of the chicken wire, and one 12 inches high and level with the outer edge of the 'roof'. To facilitate easy entry for sampling, it was found useful to arrange the lashings of the horizontal wires so that one half of the netting could be rolled back at a time, thus avoiding the need for lifting the netting off completely (Plate 12).

This netted area (Figure 1, D) gave useful results during the winter 1960–1, and in November 1961 a similar area (K) was again netted over completely to exclude all large predators. In addition, in 1961 an area (H) of the same size was marked off nearby, this time confining the netting to the roof; the edges of the netting were 12 inches from the ground and the sides were left open except for a single wire at 6 inches (Figure 5). It was hoped that this second type of netted area would not interfere with possible feeding activities of fish, while still excluding oystercatchers, and the horizontal wire was intended as an added discouragement to the entry of birds.

In 1960–1, the netted area (D) was sampled every three months until the numbers became too few for useful results; in 1961–2 the period between samples was reduced to two months. In November 1960 and February 1961 only five samples of $\frac{1}{10}$th square metre were taken inside the netting, but on subsequent occasions eight samples were taken (Figure 5 and

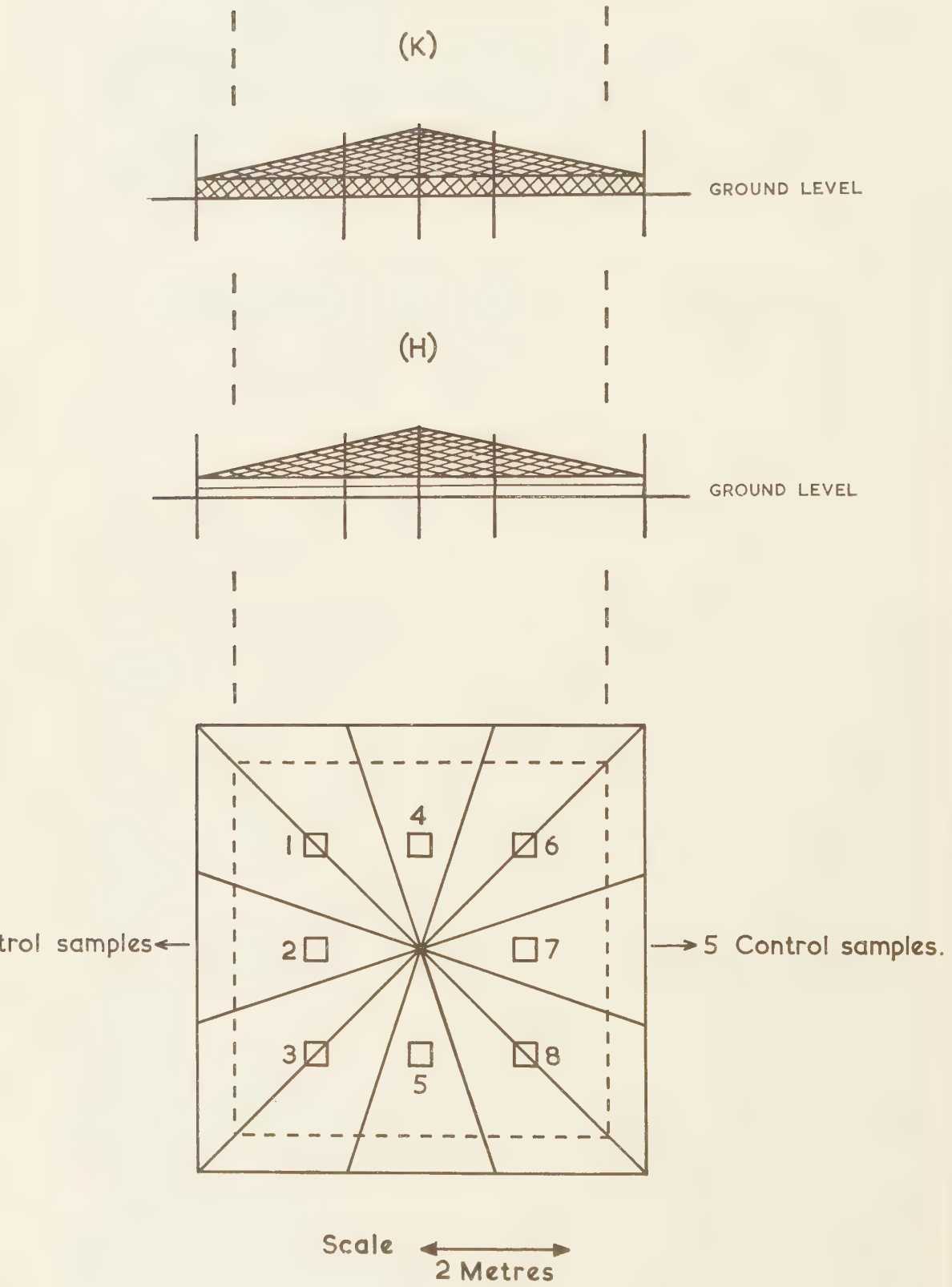


Fig. 5. *Side elevations of fenced areas covered by wire netting – (K) completely netted and (H) with open sides (see also Figure 1). Plan view shows positions of samples 1–8. Broken line shows limit of sampling area, unbroken lines show position of supporting wires. Control samples 7½ metres apart.*

PLATE 1

Wooden posts marking fenced area (A in Figure 1) erected in 1959 remained until early 1963.
Additional angle-iron stakes were added as a precautionary measure.

PLATE 2

Digging out a $\frac{1}{10}$ m² sample delimited by a metal square.

PLATE 3

Washing a sample in a $\frac{1}{8}$-inch square-meshed brass sieve by immersion in a natural water-filled depression.

PLATE 4

Transference of sieved sample into a labelled bag held open by a plastic funnel.

PLATE 5

Gulls feeding on cockles broken in hoof and wheel marks left by a horse and cart. August 1961. Note fenced area (A) in the background to the left.

PLATE 6

Typical heaps of broken shells left by oystercatchers.

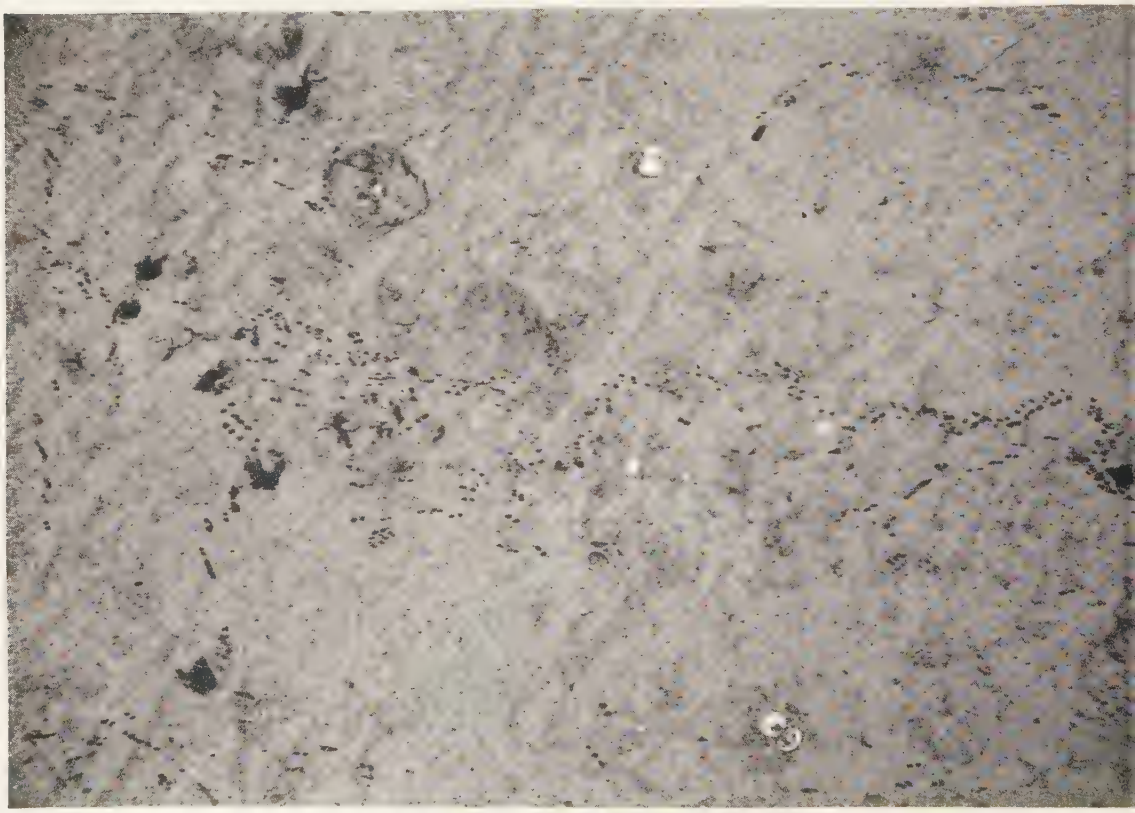
PLATE 7

Severe damage caused by oystercatchers on First Arrow bed, February 1961.

PLATE 8

Typical appearance of shells of second-winter cockles broken open by oystercatchers.

PLATE 9



Probe holes left by the open beak of an oystercatcher over an area densely populated with young cockles. Larger holes indicate the selective removal of some of the few individuals entering their second winter (August 1961).

PLATE 10

Feeding heaps left by oystercatchers inside and outside a fenced area. (The wires had been damaged recently by rough weather.)

PLATE 11

Area completely covered by wire netting to exclude large predators.

Wire netting from a completely netted area rolled back half at a time to allow sampling. Note the fenced area (A in Figure 1) without netting in the background on the right, and control samples in between.

Table 4 – Appendix I). Ten control samples, five each side, were taken on each occasion (Figure 1).

In both 1960–1 and 1961–2, netted areas erected on other parts of Llanrhidian Sands did not survive intact for more than 3 months, as a result of wave action, storm damage and accumulation of weed, which caused collapse of the angle-iron stakes, sagging and breakage of the supporting wires and collapse of the netting. On First Arrow bed, however, the netting and supports survived for at least nine months, but after this time the supporting wires started to collapse and the wire netting began to disintegrate. For prolonged observations in the same area it would be advisable to replace netting and supporting wires more frequently than at nine-monthly intervals. Netted area (K) was erected in November 1961, and by September 1962 the wire netting was becoming weak and was removed in November, but the fence was left in position and sampling was continued until May to give information on the mortality of cockles which had been protected through their second winter (Figure 6 and Table 6 – Appendix I).

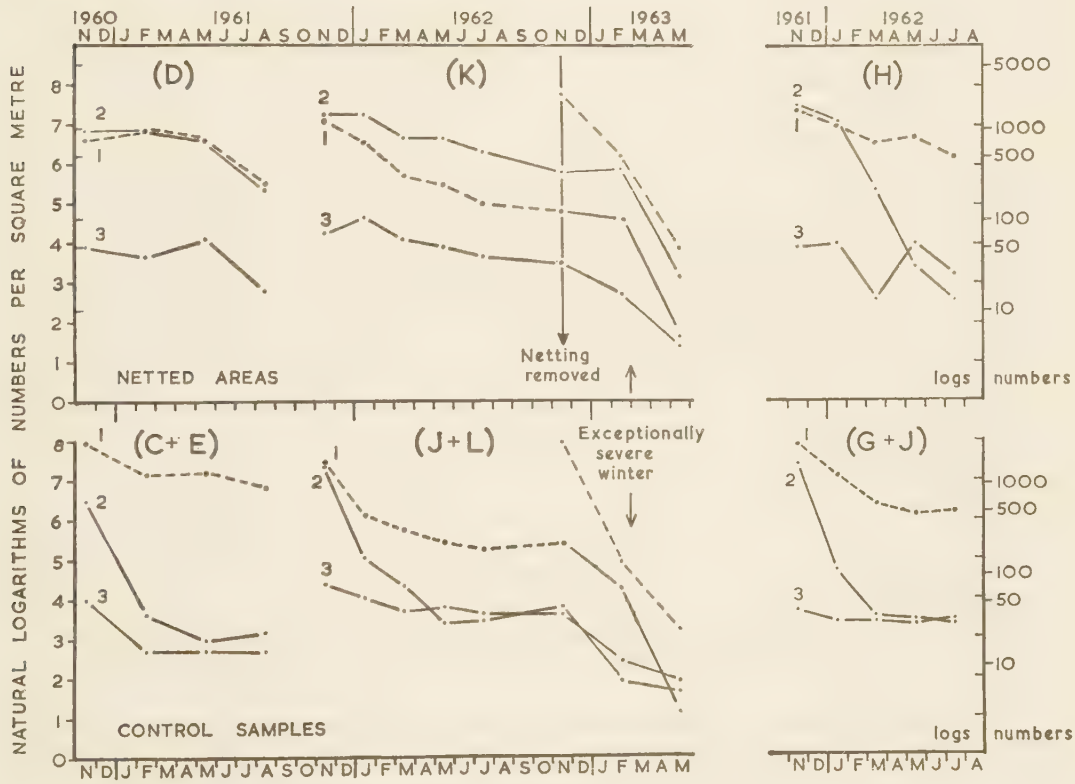


Fig. 6. *Changes in natural logarithms of numbers per square metre in areas completely protected by netting (D and K), in netted area with open sides (H), and in control samples. Broken lines denote the youngest age group in each series, i.e. commencing their first winter in November. Solid lines show age groups commencing their second* (2) *and subsequent* (3) *winters.*

RESULTS FROM NETTED AREAS

The results obtained from samples taken inside and outside the netted areas have been expressed as natural logarithms in Figure 6; in this Figure the results for the appropriate control samples for each netted area (i.e. those taken outside the area) are shown below it. These control samples gave broadly similar results to those from the fenced area (A) and its controls (B and C) (Figure 4), i.e. a much higher mortality rate amongst second-winter cockles than amongst either older or younger ones, particularly between November and

February. The results obtained inside the netted areas were quite different, and between November 1960 and May 1961 (netted area D) the loss of all age groups of cockles was negligible; between May and August 1961, however, there was a heavy loss which did not occur elsewhere. By November the wire had collapsed and its movements had interfered with the surface of the sand, so that no effective results were obtained after August in this area. In the second completely netted area (K) (Figure 6), commencing in November 1961 the loss of second-winter cockles was again greatly reduced compared with the loss in unprotected samples (J and L), while the rate of loss of both first-winter cockles and those older than second winter was essentially the same as in unprotected samples. This time an increased summer loss between May and August did not occur.

These results should be compared with those from the netted area with open sides (H) (Figure 6). Between November 1961 and January 1962, the loss of second-winter cockles was again reduced, but this was followed from January onwards by a rapid disappearance of second-winter cockles. Within the limits of sampling error, the rates of loss of other age-groups were similar inside and outside the netting.

DISCUSSION OF RESULTS FROM NETTED AREAS

The results obtained showed that a complete covering of netting afforded considerable protection for the cockles enclosed within, and the high rate of loss of second-winter cockles was reduced to negligible proportions. It should be mentioned that Davidson (pers. com.) observed oystercatchers feeding all round and close to the netted areas in December 1961.

The anomalous loss which was observed in area (D) between May and August 1961 occurred as a similar proportion amongst all age groups, and it should be remembered that during this time the originally much smaller first-winter cockles were growing fast and becoming less strikingly different in size and weight from older cockles. This isolated heavy summer loss, which was not observed in other samples, nor inside the netted area in the following year, is most likely to have arisen from unfavourable environmental conditions, probably created artificially by the presence of the netting, and it is significant that the final collapse of the netting occurred between August and November.

Other possible explanations which have been suggested for the apparent protection of cockles within the netted areas, apart from the obvious one of exclusion of large predators, include (1) an alteration in the normal physical conditions inside the netting and (2) interference with the normal movements of cockles in such a way as to encourage their retention inside the netting and reduce their dispersal from it. However, there seems to be no reason why, even supposing (1) did occur, a small change in the physical conditions, such as that suggested of slight protection afforded by the netting from wind, tide or extremes of temperature, should result in an improved survival of a selected age group of cockles; referring to (2), the movements of cockles older than first-winter on Llanrhidian Sands are considered to be negligible except under rough conditions of wind and tide. Kreger (1940) and Kristensen (1957) provide convincing evidence that migration and displacements of cockles on Dutch oyster beds are not part of the normal behaviour pattern. It should be noted also that improved survival of cockles also occurred in the netted area with open sides, in which there would be no retentive effects of the sides of the net. It is true that the numbers per sample occasionally increased between sampling dates, but this also occurred in areas not protected by netting (Figure 4) and is considered to result from errors due to sampling.

It is unfortunate that in netted area (D) erected in November 1960 the number of cockles, and particularly of first-winter cockles, was less than in the surrounding area, but that the results did not arise purely from a density effect is confirmed by the similar pattern observed in the following winter, when high densities of both first- and second-winter cockles were present inside as well as outside the netted area.

In the netted area with open sides (H), a heavy loss of second-winter cockles commenced in January 1962 (Figure 6). This is believed to have been due to the fact that oystercatchers were not completely excluded by the netting. Experienced ornithologists inspecting this area

suggested that the netting could only be expected to have the effect of reducing the entry of oystercatchers. That this is what actually happened is suggested by the fact that the loss of second-winter cockles between November and January, although much less than that outside, was still much greater than in completely netted area (K). By January 1962, the average density of second-winter cockles outside netted area (H) had become reduced to less than 100 per square metre, while cockles inside were still present at more than 1,100 per square metre. This small area of high density might well then have supplied an attraction which overcame the reluctance of oystercatchers to enter the area, with the resulting rapid disappearance of most of the cockles. Since constructing this netted area without sides it has been learned that a similar device is sometimes used as a bird trap, in which a wire roof drops over the prey (Harris, pers. com.). On another part of the cockle beds a similar area was roofed over by a 'spider's web' of P.V.C.-covered wire, and this not only failed to reduce the loss of cockles inside, but bird feet marks and droppings were observed inside the area. The possibility that the heavy mortality in netted area (H) was caused by fish was discounted in view of the evidence given in an earlier section.

The survival of cockles to a density of more than 300 per square metre during their third winter was the highest recorded in all the surveys of this area of Llanrhidian Sands (Appendix I, Tables 2 and 3). This density occurred in netted area (K) from which fishermen and large predators had been excluded until the netting, but not the fencing, was removed in November 1962. The survival of these cockles remained good during the winter months between November and February 1963, but then the effects of the extremely severe winter reduced the numbers of all age groups to negligible proportions. It is interesting that the survival of second-winter cockles (Figure 6 and Table 6) between November 1962 and February 1963 was also good in area (K), but this is believed to have been due to their low density (121 per square metre) compared with other areas of greater density such as fenced area (A) (over 600 per square metre) and elsewhere, where a high mortality rate amongst second-winter cockles was recorded as usual (Figure 4). It is also known that during that winter oystercatchers were feeding on cockles which had been weakened by the severe cold and exposed on the surface of the sand.

In Appendix III, the results from netted areas have been examined for statistical significance, and compared with the results from the fenced area without netting, and unprotected control areas. The losses of second-winter cockles from netted areas in both years were highly significantly less than from unprotected control areas.

It was not possible to make a quantitative estimate of the losses attributable to oystercatchers from the area of First Arrow bed, separately from the whole cockle bed, because the number of cockles removed by fishing from this area cannot be separated reliably from the total landings. In any case, an estimate of oystercatcher damage to the First Arrow bed need not be representative of the whole cockle bed, because the birds are completely mobile and may feed more heavily in some areas than others. However, in a later paper, these results will be combined with those from fenced areas and transect surveys over other parts of Llanrhidian Sands to provide a quantitative assessment of losses from various causes.

SUMMARY AND CONCLUSIONS

1. The examination of samples of cockles from Llanrhidian Sands cockle beds showed the unusually high mortality rate of 91% for cockles during their second winter, compared with 48% during their first winter and less than 20% for older cockles. In each case the mortality figure refers to the 3-monthly period from mid-November to mid-February.
2. This pattern of mortality was known to be unconnected with fishing for cockles because it was observed also inside an area fenced off to prohibit fishing.
3. The various possible causes of natural mortality have been discussed, and it was concluded that unfavourable environmental conditions and parasites or diseases could not be held to be responsible for causing much greater losses of second-winter cockles than either younger or older ones.

4. It was decided that the most likely cause was selective feeding by a predator. Fish (flounders) occur in large numbers but they were found to feed only on the smallest cockles and mainly during the summer months, so that although they may account for a large number of young cockles, they are not likely to be responsible for the heavy loss of cockles during their second winter.
5. The results of observations on the numbers and feeding behaviour of oystercatchers provided a convincing explanation for the loss of second-winter cockles, and in netted areas from which the birds were excluded the loss of second-winter cockles was greatly reduced.
6. In the present account only the methods used for examining and identifying the causes of natural mortality have been described. The results obtained from this selected portion of the cockle beds will later be combined with those from the remaining area of Llanrhidian Sands in order to make a quantitative assessment of losses from various causes over the whole cockle bed.

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APPENDIX I

Numbers of cockles of different ages in $\frac{1}{10}$ m² samples from sampling areas shown in Figures 1, 2 and 5. The numbers which settled in each summer have been traced through subsequent samples from areas protected by fencing or netting and their control areas. These results have been shown in Figures 3, 4, 6 and 7. At the end of each second winter the numbers surviving were small, and they have been added to the numbers of older cockles surviving from previous years' settlements. NT = not taken. [ ] = estimated.

Table 2. FENCED AREA (A) and ITS CONTROL AREAS (B) AND (C)

	FENCED AREA (A) – SAMPLES 1–10												CONTROL AREA (C) SAMPLES 11–15					CONTROL AREA (B) SAMPLES 16–20						
Date	1	2	3	4	5	6	7	8	9	10	Total	$\log_e$	11	12	13	14	15	16	17	18	19	20	Total in 10 samples	$\log_e$
(a) Cockles which settled before summer 1958																								
November 1958	5	8	6	2	2	1	2	2	2	13	43	3·76	39	9	6	20	6	8	14	15	13	3	133	4·89
February 1959	1	5	13	1	3	3	6	13	2	15	62	4·13	10	9	5	5	0	11	4	9	13	3	69	4·23
April 1959	16	5	17	2	3	1	5	8	9	12	78	4·36	22	10	15	12	4	2	5	9	7	7	93	4·53
July 1959	8	11	15	16	6	6	6	6	5	1	80	4·38	9	3	0	5	0	14	9	4	10	9	63	4·14
November 1959	5	6	14	6	4	3	1	4	6	3	52	3·95	5	3	4	2	5	9	4	3	0	0	35	3·56
February 1960	2	6	6	2	4	4	4	2	2	6	38	3·64	9	3	3	7	0	5	1	3	1	5	37	3·61
April 1960	10	0	10	0	4	1	9	1	3	8	46	3·83	4	1	3	4	1	5	2	5	4	1	30	3·40
From April 1960, these numbers were added to those of survivors from the 1958 settlement (see para. (b)).																								
(b) Cockles which settled in summer 1958																								
November 1958	443	147	115	235	196	284	270	143	193	247	2,273	7·73	297	270	89	233	285	163	392	80	114	50	1,973	7·59
February 1959	98	122	125	95	67	103	64	171	83	136	1,064	6·97	97	84	202	85	50	92	71	55	39	39	814	6·70
April 1959	79	119	169	85	116	135	79	54	52	104	992	6·90	73	83	53	69	95	46	97	38	12	15	581	6·36
July 1959	117	137	137	106	112	82	139	75	78	99	1,082	6·99	70	50	46	73	82	77	60	49	39	11	557	6·32
November 1959	75	80	99	82	163	104	109	60	74	95	941	6·85	95	77	76	111	76	32	44	28	21	17	577	6·36
February 1960	11	8	6	4	3	6	4	4	6	6	58	4·06	7	7	6	13	3	2	6	1	2	5	52	3·95
April 1960	9	2	3	6	2	3	3	3	4	4	39	3·66	5	3	8	14	2	7	5	10	3	6	63	4·14
Because the numbers are now small to these have been added the numbers of cockles surviving from settlement before 1958.																								
April 1960	19	2	13	6	6	4	12	4	7	12	85	4·44	9	4	11	18	3	12	7	15	7	7	93	4·53
August 1960	22	8	9	11	11	12	9	13	4	6	105	4·65	15	4	9	11	4	14	11	3	9	8	88	4·48
November 1960	6	2	9	10	3	7	4	10	9	4	64	4·16	8	2	4	2	11	8	6	7	4	7	59	4·08
February 1961	5	5	6	0	5	0	3	5	6	2	37	3·61	3	0	0	3	0	3	3	11	2	6	31	3·43
May 1961	3	2	3	0	4	5	5	5	1	6	34	3·53	2	4	0	2	2	5	3	2	7	5	32	3·47
(c) Cockles which settled in summer 1959																								
November 1959	260	349	230	415	203	311	284	262	311	365	2,990	8·00	215	292	167	123	279	117	223	238	452	280	2,386	7·78
February 1960	239	240	108	239	130	117	157	158	138	111	1,637	7·40	74	101	109	212	209	57	126	66	289	63	1,306	7·17
April 1960	135	91	122	170	86	134	94	114	95	70	1,111	7·01	91	77	93	136	170	101	78	136	115	153	1,150	7·05
August 1960	113	121	70	116	73	96	53	83	78	66	869	6·77	42	46	77	105	106	44	93	57	161	62	793	6·68
November 1960	104	108	66	115	92	80	53	114	116	58	906	6·81	68	80	58	22	140	77	22	47	29	13	556	6·32
February 1961	4	2	2	7	11	2	2	4	4	16	54	3·99	0	2	2	0	0	0	1	3	11	4	23	3·14
May 1961	4	3	7	5	4	2	1	2	0	5	33	3·50	1	0	3	1	1	2	2	1	5	9	25	3·22

Table 2—cont.

Date	1	2	3	4	5	6	7	8	9	10	Total	$\log_e$	11	12	13	14	15	16	17	18	19	20	Total in 10 samples	$\log_e$
May 1961	7	5	10	5	8	7	6	7	1	11	67	4·20	3	4	3	3	3	7	5	3	12	14	57	4·04
August 1961	2	6	5	6	6	10	7	7	6	8	63	4·14	5	2	1	2	6	6	5	9	5	6	47	3·85
November 1961	3	4	1	1	2	1	2	3	5	6	28	3·33	2	1	4	0	3	6	3	8	6	4	37	3·61
January 1962	5	5	6	8	2	0	4	4	2	3	39	3·66	4	6	0	0	2	4	2	0	5	[3]	26	3·26
March 1962	5	2	1	0	1	2	3	1	6	2	23	3·14	9	5	2	0	2	3	7	5	5	5	43	3·76
May 1962	5	5	4	5	1	5	4	3	4	3	39	3·66	3	1	1	3	2	3	2	0	2	6	23	3·14
(*d*) *Cockles which settled in summer* 1960																								
November 1960	513	534	405	576	623	599	550	537	555	568	5,460	8·61	539	468	317	502	332	252	160	262	38	56	2,926	7·98
February 1961	71	46	297	309	357	86	134	459	416	371	2,546	7·84	132	207	266	131	118	73	152	21	12	22	1,134	7·03
May 1961	84	220	322	243	344	110	281	357	319	291	2,571	7·85	264	238	167	238	226	99	110	19	86	65	1,512	7·32
August 1961	263	66	239	123	242	233	210	274	308	261	2,219	7·70	49	161	111	143	177	64	64	38	76	103	986	6·89
November 1961	125	67	37	178	226	33	54	273	197	193	1,383	7·23	201	114	129	145	118	25	14	6	6	26	784	6·66
January 1962	0	10	12	8	5	3	19	3	3	3	66	4·19	2	1	0	3	5	21	19	4	0	[11]	66	4·19
March 1962	1	2	3	5	4	2	18	3	5	5	48	3·87	5	10	2	3	0	15	7	4	5	4	55	4·01
May 1962	1	3	1	0	0	4	6	2	1	0	18	2·89	7	2	2	3	7	5	3	4	0	8	41	3·71
To these have been added the numbers surviving from settlement before 1960.																								
May 1962	6	8	5	5	1	9	10	5	5	3	57	4·04	10	3	3	6	9	8	5	4	2	14	64	4·16
July 1962	8	9	10	10	5	2	6	8	10	12	80	4·38	3	3	4	3	3	0	7	3	11	7	44	3·78
September 1962	1	12	7	1	5	5	4	4	4	8	51	3·93	7	0	1	4	1	5	2	3	4	2	29	3·37
November 1962	1	2	5	1	6	6	6	1	5	8	41	3·71	7	3	2	3	6	4	0	1	6	3	35	3·56
February 1963	0	3	3	0	1	4	0	0	1	1	13	2·56	1	4	0	1	3	1	2	2	1	0	15	2·71
(*e*) *Cockles which settled in summer* 1961																								
August 1961	261	728	109	310	206	361	345	137	93	127	2,677	7·89	NOT COUNTED											
November 1961	369	418	156	220	131	184	42	123	192	176	2,011	7·61	175	604	125	361	358	137	53	412	429	522	3,176	8·06
January 1962	98	117	70	83	33	122	49	66	45	68	751	6·62	134	248	16	150	120	80	137	84	373	[520]	1,862	7·53
March 1962	172	287	56	65	77	116	62	51	68	47	1,001	6·91	102	63	143	23	101	163	169	226	292	515	1,797	7·49
May 1962	102	195	118	56	66	106	79	57	67	59	905	6·81	140	82	81	62	133	114	122	77	206	164	1,181	7·07
July 1962	113	181	82	64	75	109	86	53	46	65	874	6·77	124	103	51	40	158	71	110	86	226	190	1,159	7·06
September 1962	108	186	87	61	62	65	76	46	44	52	787	6·67	78	87	58	91	175	82	59	50	96	135	911	6·81
November 1962	47	64	58	48	76	79	50	52	57	76	607	6·41	113	67	46	60	90	56	30	71	78	77	688	6·53
February 1963	0	7	1	5	5	8	0	7	4	2	39	3·66	7	7	3	9	71	1	3	4	1	2	108	4·68
(*f*) *Cockles which settled in summer* 1962																								
September 1962	89	87	114	130	88	89	124	159	117	130	1,127	7·03	NOT COUNTED											
November 1962	161	140	146	196	235	201	164	195	187	185	1,810	7·50	259	112	164	194	240	46	32	26	20	12	1,105	7·01
February 1963	3	0	5	7	1	1	3	20	11	5	56	4·03	5	19	3	16	27	0	0	5	0	1	76	4·33

Table 3. CONTROL SAMPLES FROM TRANSECT (F)

Date	SAMPLES 1–17																	Total	Average per sq. m.	$\log_e$
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17			
(a) Cockles which settled before summer 1958																				
November 1958	0	0	2	3	6	3	0	4	10	9	2	15	3	30	10	12	6	115	68	4·22
February 1959	0	2	4	1	1	0	1	7	4	16	12	9	10	8	19	5	NT	99	62	4·13
May 1959	0	1	4	1	0	1	2	4	2	6	7	3	4	10	14	2	2	63	37	3·61
July 1959	0	0	0	2	1	2	2	2	5	8	16	7	11	3	3	3	8	73	43	3·76
November 1959	0	1	0	0	0	2	0	3	5	5	8	13	0	0	2	12	0	51	30	3·40
February 1960	NOT TAKEN						1	1	1	8	4	3	1	11	2	1	0	33	[21]	[3·04]
May 1960	0	0	1	0	1	1	0	0	3	3	4	6	7	7	3	1	0	37	22	3·09
From May 1960, these numbers were added to those of survivors from the 1958 settlement (see para. (b)).																				
(b) Cockles which settled in summer 1958																				
November 1958	26	60	84	69	87	42	71	79	57	80	15	160	124	202	263	829	443	2,691	1,583	7·37
February 1959	33	22	44	44	26	22	32	41	38	64	18	63	118	183	237	244	NT	1,229	768	6·64
May 1959	18	16	11	40	34	33	29	27	38	34	45	23	65	72	102	122	59	768	452	6·11
July 1959	1	27	19	19	25	28	22	26	37	53	64	34	60	72	79	76	148	790	465	6·14
November 1959	17	13	8	17	14	17	13	11	3	19	3	12	64	55	37	93	13	409	241	5·48
February 1960	NOT TAKEN						0	4	3	1	3	4	3	13	1	12	5	49	[36]	[3·58]
May 1960	0	1	0	0	0	7	5	6	4	4	3	8	24	2	7	16	0	87	51	3·93
To these have been added the numbers surviving from settlement before 1958.																				
May 1960	0	1	1	0	1	8	5	6	7	7	7	14	31	9	10	17	0	124	73	4·29
August 1960	0	0	6	3	0	1	4	3	4	10	14	9	4	4	3	21	2	88	52	3·95
November 1960	0	3	0	2	5	3	5	5	10	3	7	2	11	8	5	8	1	78	46	3·83
February 1961	NT	0	0	2	2	1	3	0	6	8	8	6	4	1	2	1	1	45	28	3·33
May 1961	NT	2	2	1	3	2	2	2	3	1	8	5	5	10	1	2	0	49	31	3·43
(c) Cockles which settled in summer 1959																				
November 1959	55	130	67	27	33	45	28	36	30	79	188	244	319	316	324	123	10	2,054	1,208	7·10
February 1960	NOT TAKEN						31	35	63	79	85	114	214	221	104	77	11	1,034	[737]	[6·60]
May 1960	6	10	29	17	9	12	17	30	26	49	106	181	135	94	44	53	2	820	482	6·18
August 1960	2	2	10	8	8	15	22	12	35	46	55	141	84	74	39	76	0	629	370	5·91
November 1960	1	5	6	1	2	7	5	9	9	70	113	99	72	56	39	36	8	538	316	5·76
February 1961	NT	0	1	0	1	0	0	3	4	3	10	2	0	1	2	3	3	33	21	3·04
May 1961	NT	0	0	0	1	1	2	2	2	4	6	1	2	1	0	6	2	30	19	2·94
To these have been added the numbers surviving from settlement before 1959.																				

ıble 3—*cont.*

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total	Average per sq. m.	$\log_e$
May 1961	NT	2	2	1	4	3	4	4	5	5	14	6	7	11	1	8	2	79	50	3·91
August 1961	0	1	2	6	1	2	2	5	7	9	9	3	6	2	2	1	0	58	34	3·53
November 1961	0	0	2	3	3	2	2	4	5	3	9	1	9	11	4	9	2	69	41	3·71
January 1962	0	0	0	2	5	1	3	10	3	8	7	4	2	2	1	2	0	50	29	3·37
March 1962	0	0	2	1	3	2	3	5	4	2	5	2	6	6	3	1	0	45	26	3·26
May 1962	0	0	0	1	1	2	2	1	5	6	7	2	7	4	2	2	1	43	25	3·22
(*d*) *Cockles which settled in summer* 1960																				
November 1960	106	117	109	91	88	113	62	38	28	141	216	251	434	393	352	12	4	2,555	1,503	7·32
February 1961	NT	61	55	36	47	44	90	104	88	78	94	67	104	70	166	3	11	1,118	699	6·55
May 1961	NT	27	26	31	35	46	67	66	53	69	67	86	90	197	24	8	5	897	561	6·33
August 1961	8	8	20	32	16	27	36	51	57	73	81	62	54	202	89	7	3	826	486	6·19
November 1961	0	11	11	7	12	17	8	23	13	40	57	15	72	60	28	11	3	388	228	5·43
January 1962	3	5	6	6	7	6	5	8	9	4	7	17	4	2	0	6	5	100	59	4·08
March 1962	0	2	2	2	4	4	3	2	4	11	2	6	7	2	10	3	2	66	38	3·64
May 1962	0	2	2	3	1	1	2	5	4	4	4	5	5	4	2	2	1	47	28	3·33
To these have been added the numbers surviving from settlement before 1960.																				
May 1962	0	2	2	4	2	3	4	6	9	10	11	7	12	8	4	4	2	90	53	3·97
July 1962	NT	1	6	3	6	11	10	9	4	12	15	8	2	9	2	7	0	105	62	4·13
September 1962	2	0	2	5	2	3	11	11	10	10	13	12	7	12	6	9	3	118	69	4·23
November 1962	0	3	4	1	4	8	5	8	10	10	7	6	3	3	4	9	10	95	56	4·03
February 1963	0	1	0	2	3	3	0	6	5	1	5	0	0	2	0	2	1	31	18	2·89
(*e*) *Cockles which settled in summer* 1961																				
August 1961	9	31	22	13	4	17	10	56	72	9	42	299	365	508	486	34	637	2,614	1,538	7·34
November 1961	3	26	5	3	11	10	12	20	32	40	156	90	368	113	179	48	364	1,480	871	6·77
January 1962	3	2	6	2	13	8	26	20	33	68	43	134	95	76	329	70	387	1,315	774	6·65
March 1962	2	0	1	0	0	3	4	18	18	60	84	72	154	146	127	105	284	1,078	634	6·45
May 1962	0	0	2	2	3	9	6	15	25	33	62	63	62	115	130	155	219	901	530	6·27
July 1962	NT	1	0	8	0	4	10	16	32	18	29	45	101	78	122	97	67	628	369	5·91
September 1962	1	0	2	1	2	2	2	16	22	10	26	62	53	65	107	102	211	684	402	6·00
November 1962	1	0	5	0	3	1	10	5	15	20	30	62	47	67	104	96	148	614	361	5·89
February 1963	1	1	1	2	0	4	5	3	10	5	19	1	1	0	1	11	1	66	39	3·66
(*f*) *Cockles which settled in summer* 1962																				
November 1962	60	65	57	20	34	22	33	66	39	63	133	97	109	207	72	74	33	1,184	696	6·55
February 1963	1	2	3	2	5	9	17	9	20	18	25	3	2	1	0	3	0	120	71	4·26

Table 4. NETTED AREA (D) AND ITS CONTROL SAMPLES (C AND E) – 1960–1

Only 5 samples were taken inside the netted area, until May 1961 when 8 samples were taken.

Date	NETTED AREA (D) SAMPLES 1–8											CONTROL SAMPLES (C) 11–15					CONTROL SAMPLES (E) 1–5						
	1	2	3	4	5	6	7	8	Total	Average per sq. m.	$\log_e$	11	12	13	14	15	1	2	3	4	5	Total in 10 samples	$\log_e$
(a) Cockles which had settled in summer 1960, i.e. first-winter cockles																							
November 1960	109	73	75	71	29	—	—	—	357	714	6·57	539	468	317	502	332	85	30	69	99	377	2,818	7·94
February 1961	142	109	48	82	60	–	—	—	441	882	6·78	132	207	266	131	118	37	52	66	223	34	1,266	7·14
May 1961	47	81	73	126	75	70	89	40	601	751	6·62	264	238	167	238	226	58	27	19	50	79	1,366	7·22
August 1961	39	35	63	14	14	3	20	5	193	241	5·48	49	161	111	143	177	26	20	47	51	73	858	6·75
(b) Cockles which had settled in summer 1959, i.e. second-winter cockles																							
November 1960	97	135	57	111	73	—	—	—	473	946	6·85	68	80	58	22	140	54	36	56	39	119	672	6·51
February 1961	61	115	50	87	116	–	—	—	429	858	6·75	0	2	2	0	0	3	6	15	5	4	37	3·61
May 1961	33	111	87	105	57	82	108	26	609	761	6·63	1	0	3	1	1	0	2	3	4	4	19	2·94
August 1961	Samples not examined separately								169	211	5·35	Samples not examined separately										23	3·14
(c) Cockles which had settled before summer 1959																							
November 1960	6	7	6	0	5	—	—	—	24	48	3·87	8	2	4	2	11	3	3	13	2	7	55	4·01
February 1961	4	1	3	3	8	—	—	—	19	38	3·64	3	0	0	3	0	1	2	5	0	0	14	2·64
May 1961	2	7	5	11	2	6	8	6	47	59	4·08	2	4	0	2	2	1	1	2	0	1	15	2·71
August 1961	Samples not examined separately								13	16	2·77	Samples not examined separately										13	2·56

Table 5. NETTED AREA WITH OPEN SIDES (H) AND ITS CONTROL SAMPLES (G) AND (J) – 1961–2

Date	NETTED AREA (H) SAMPLES 1–8											CONTROL SAMPLES (G) 1–5					CONTROL SAMPLES (J) 1–5						
	1	2	3	4	5	6	7	8	Total	Average per sq. m.	$\log_e$	1	2	3	4	5	1	2	3	4	5	Total in 10 samples	$\log_e$
(*a*) *Cockles which settled in summer* 1961, *i.e. first-winter cockles*																							
November 1961	192	110	174	104	215	124	120	239	1,278	1,598	7·38	520	342	254	363	181	168	157	249	149	335	2,718	7·91
January 1962	126	126	117	75	83	92	112	168	899	1,124	7·03	250	254	72	212	101	88	36	46	66	71	1,196	7·09
March 1962	38	54	78	50	78	41	62	148	549	686	6·53	30	124	37	97	74	81	33	34	32	40	582	6·37
May 1962	101	89	114	75	62	53	NT	90	584	834	6·73	59	87	45	77	36	31	40	22	24	31	452	6·11
July 1962	58	46	71	50	47	32	38	41	383	479	6·17	99	92	60	42	50	29	27	20	30	35	484	6·18
(*b*) *Cockles which settled in summer* 1960, *i.e. second-winter cockles*																							
November 1961	202	94	191	233	181	219	152	185	1,457	1,821	7·51	65	135	190	181	135	199	235	203	131	115	1,589	7·37
January 1962	156	109	123	87	182	125	49	91	922	1,153	7·05	7	4	2	3	17	17	10	8	29	16	113	4·73
March 1962	25	9	28	31	15	19	10	34	171	214	5·37	0	8	2	2	5	2	4	6	1	5	35	3·56
May 1962	3	2	5	5	0	5	2	2	24	30	3·40	3	3	4	3	0	0	7	3	8	1	32	3·47
July 1962	3	1	3	1	0	0	1	1	10	13	2·57	6	4	0	3	1	0	4	4	2	5	29	3·37
(*c*) *Cockles which settled before summer* 1960																							
November 1961	1	5	3	7	4	4	13	2	39	49	3·89	0	2	0	0	3	6	7	6	6	8	38	3·64
January 1962	5	7	2	6	4	10	3	7	44	55	4·01	1	1	1	1	7	2	3	5	4	4	29	3·37
March 1962	0	0	0	4	1	2	1	2	10	13	2·57	1	0	1	5	6	3	2	1	9	1	29	3·37
May 1962	6	4	5	3	4	6	6	8	42	53	3·97	0	1	1	3	1	4	5	4	4	5	28	3·33
July 1962	1	2	3	3	4	0	2	4	19	24	3·18	3	2	1	1	7	2	4	1	3	7	31	3·43

Table 6. NETTED AREA (K) AND ITS CONTROL SAMPLES (J AND L) – 1961–2

The netting was removed from this area after sampling in November 1962, but the area was still marked by stakes and wire, and sampling continued until May 1963.

Date	NETTED AREA (K) SAMPLES 1–8											CONTROL SAMPLES (J) 1–5					CONTROL SAMPLES (L) 1–5						
	1	2	3	4	5	6	7	8	Total	Average per sq. m.	$\log_e$	1	2	3	4	5	1	2	3	4	5	Total in 10 samples	$\log_e$
(a) Cockles which settled in summer 1961, *i.e. first-winter cockles*																							
November 1961	130	186	134	118	129	64	62	121	944	1,180	7·07	168	157	249	149	335	105	127	131	130	150	1,701	7·44
January 1962	108	73	54	38	78	94	54	58	557	696	6·55	88	36	46	66	71	21	21	70	11	19	449	6·11
March 1962	43	30	29	22	26	33	17	41	241	301	5·71	81	33	34	32	40	26	24	14	17	17	318	5·76
May 1962	33	18	15	29	19	21	34	17	186	233	5·45	31	40	22	24	31	19	11	17	14	12	221	5·40
July 1962	13	10	22	20	15	13	15	13	121	151	5·02	29	27	20	30	35	15	13	4	13	6	192	5·26
November 1962	22	4	10	21	14	6	14	6	97	121	4·80	33	33	25	39	30	20	8	7	10	14	219	5·39
Netting removed																							
February 1963	8	12	7	10	13	7	13	11	81	101	4·62	12	9	10	14	5	0	4	5	5	10	74	4·30
May 1963	0	1	0	0	1	2	0	0	4	5	1·61	0	0	0	0	0	3	0	0	0	0	3	1·10
(b) Cockles which settled in summer 1960, *i.e. second-winter cockles*																							
November 1961	145	115	120	129	149	168	148	173	1,147	1,434	7·27	199	235	203	131	115	139	210	88	118	180	1,618	7·39
January 1962	126	113	105	98	162	162	153	194	1,113	1,391	7·24	17	10	8	29	16	15	25	12	6	15	153	5·03
March 1962	83	63	106	31	57	133	50	88	611	764	6·64	2	4	6	1	5	12	12	17	2	15	76	4·33
May 1962	74	42	81	111	75	108	47	82	620	775	6·65	0	7	3	8	1	1	2	3	2	1	28	3·33
July 1962	56	51	48	52	37	51	106	39	440	550	6·31	0	4	4	2	5	1	4	6	4	1	31	3·43
November 1962	59	11	29	43	24	35	46	14	261	326	5·79	4	5	2	4	1	7	6	10	3	2	44	3·78
Netting removed																							
February 1963	39	59	36	34	32	25	39	23	287	359	5·88	1	1	0	2	1	0	0	0	0	2	7	1·95
May 1963	4	1	2	6	1	1	2	1	18	23	3·14	0	0	1	2	0	1	0	0	1	0	5	1·61
(c) Cockles which settled before summer 1960																							
November 1961	9	9	4	4	11	3	10	6	56	70	4·25	6	7	6	6	8	11	10	10	14	3	81	4·39
January 1962	8	15	19	17	7	8	5	4	83	104	4·64	2	3	5	4	4	16	8	7	3	2	54	3·99
March 1962	7	4	3	4	5	14	3	7	47	59	4·08	3	2	1	9	1	7	0	4	5	6	38	3·64
May 1962	2	3	5	7	8	4	7	4	40	50	3·91	4	5	4	4	5	2	3	9	1	8	45	3·81
July 1962	3	5	3	4	0	6	4	5	30	38	3·64	2	4	1	3	7	7	1	4	1	6	36	3·58
November 1962	7	1	2	4	3	2	6	1	26	33	3·50	4	7	6	2	5	1	1	8	3	2	39	3·66
Netting removed																							
February 1963	0	4	0	3	1	1	2	1	12	15	2·71	2	1	1	3	0	1	1	1	0	1	11	2·40
May 1963	1	0	0	1	0	0	1	0	3	4	1·39	0	1	0	0	1	0	0	1	1	3	7	1·95
(d) Cockles which settled in summer 1962																							
November 1962	314	227	258	247	260	163	216	181	1,866	2,333	7·76	240	183	277	353	334	384	238	277	250	281	2,817	7·94
February 1963	49	51	42	70	45	24	43	35	359	449	6·11	12	12	6	18	12	2	5	25	18	22	132	4·88
May 1963	10	8	4	2	4	4	4	4	40	50	3·91	2	7	1	0	2	0	2	3	8	7	32	3·47

APPENDIX II

INSTANTANEOUS MORTALITY COEFFICIENTS AND MEAN PERCENTAGE LOSSES OF COCKLES OF DIFFERENT AGES EXPRESSED, FOR COMPARISON, AS AVERAGES FOR THREE-MONTHLY PERIODS

Instantaneous total mortality coefficients (Z) have been calculated from numbers and natural logarithms shown in Appendix I, using the expression

$$N_t = N_0 e^{-Zt} \quad \text{(Beverton and Holt, 1956),}$$

where N_0 and N_t are the numbers present at the beginning and end of time t. After conversion of numbers to natural logarithms, Zt becomes equal to $\log_e N_0 - \log_e N_t$ (see also Appendix III). One advantage of working with instantaneous coefficients is that their values over consecutive periods of time can be added directly, whereas percentage mortalities cannot. In the following tables, values of Zt are expressed for three-monthly periods, i.e. $t = \frac{1}{4}$, and corresponding percentage mortalities have been calculated from them using standard e^{-x} tables, and the relationship $N_t = N_0 e^{-Zt}$. Index letters, in brackets, refer to sampling sites shown in Figure 1. Control areas B, C and F may have received varying intensities of fishing (i.e. $Z = F + M$, where Z, F and M are instantaneous total, fishing and natural mortality coefficients respectively). Fenced area (A) will have been subjected to natural mortality only, i.e. $Z = M$. The results obtained from inside and outside the fenced area were usually so similar (i.e. suggesting that very little fishing had occurred in this area) that mean values have been calculated and shown for comparison.

NB. In the winter of 1961–2, observations were made in January and March, but not in February as in previous years. The mean values of Zt shown in section A (1 and 2), following, have been calculated as a proportion of the values for the period November–March, i.e. on the assumption that the monthly values approximate to a straight line (see also Figure 4). For second-winter cockles (section B) the same procedure would have underestimated the value of Z, because the greater part of the heavy winter mortality had already occurred between November and January. Here, therefore, the value of Zt for the November–January period has been used and increased by half the loss between January and March, i.e. the mean of Zt for the two periods November–January and November–March.

A. LOSSES DURING THE PERIOD BEFORE THE SECOND WINTER

1. *First-winter cockles – losses between November and February*

Location of samples	1958–9		1959–60		1960–1		1961–2		*Mean*	
	Zt	%	Zt	%	Zt	%	Zt	%	Zt	%
Fenced area (A)	0·76	53	0·60	45	0·76	53	0·53	41	0·66	48
Controls (B + C)	0·89	59	0·61	46	0·95	61	0·43	35	0·72	51
Controls (F)	0·73	52	0·50	39	0·77	54	0·24	21	0·56	43
Mean	0·79	55	0·57	43	0·83	56	0·40	33	0·65	48

2. *Losses expressed as means per three months during the subsequent February to November*

Location of samples	1959		1960		1961		1962		*Mean*	
	Zt	%	Zt	%	Zt	%	Zt	%	Zt	%
Fenced area (A)	0·04	4	0·20	18	0·20	18	0·19	17	0·16	15
Controls (B + C)	0·11	10	0·28	24	0·12	11	0·36	30	0·22	20
Controls (F)	0·39	32	0·28	24	0·37	31	0·21	19	0·31	27
Mean	0·18	16	0·25	22	0·23	21	0·25	22	0·23	21

3. *Losses expressed as means per three months during the whole year above, i.e. November to November*

Location of samples	1958–9		1959–60		1960–1		1961–2		*Mean*	
	Zt	%	Zt	%	Zt	%	Zt	%	Zt	%
Fenced area (A)	0·22	20	0·30	26	0·35	30	0·30	26	0·29	25
Controls (B + C)	0·31	27	0·36	30	0·33	28	0·38	32	0·35	30
Controls (F)	0·47	37	0·34	29	0·47	37	0·22	20	0·38	32
Mean	0·33	28	0·33	28	0·38	32	0·30	26	0·34	29

B. LOSSES DURING THREE SECOND-WINTER MONTHS – NOVEMBER TO FEBRUARY

Location of samples	1959–60		1960–1		1961–2		*Mean*	
	Zt	%	Zt	%	Zt	%	Zt	%
Fenced area (A)	2·79	94	2·82	94	3·20	96	2·94	95
Controls (B + C)	2·41	91	3·18	96	2·56	92	2·72	93
Controls (F)	1·90	85	2·72	93	1·57	79	2·06	87
Mean	2·37	91	2·91	95	2·44	91	2·57	92

C. LOSSES FOLLOWING THE SECOND WINTER

(*i*) *Losses expressed as means per three months during the subsequent February to February*

The numbers of cockles surviving their second winter were small, so that here cockles of all ages which had survived at least until the February of their second winter, from the fenced area and its control samples, were grouped together. The annual value of Z was found by regression of natural logarithms of grouped samples taken throughout each year. Mean three-monthly values are given in the following table to compare with sections A and B (above).

Combined samples	*Feb.* 1959–*Feb.* 1960		*Feb.* 1960–*Feb.* 1961		*Feb.* 1961–*Feb.* 1962		*Mean*	
	Zt	%	Zt	%	Zt	%	Zt	%
A, B, C, F.	0·20	18	0·22	20	0·20	18	0·21	19

(*ii*) *Means per three months during November to November*

The following results from grouped samples include all ages of cockles which had survived at least until the November following the second winter.

Combined samples	*Nov.* 1959–*Nov.* 1960		*Nov.* 1960–*Nov.* 1961		*Nov.* 1961–*Nov.* 1962		*Mean*	
	Zt	%	Zt	%	Zt	%	Zt	%
A, B, C, F.	0·05	5	0·25	22	0·11	10	0·14	13

D. SUMMARY OF MEAN LOSSES PER THREE-MONTHLY PERIODS

	Fenced area (A) only		*Mean of areas* A, B, C, F	
	Zt	%	Zt	%
First winter after settlement (November to February)	0·66	48	0·65	48
Second summer after settlement (February to November)	0·16	15	0·23	21
Second winter after settlement (November to February)	2·94	95	2·57	92
Year following second winter (February to February)	→	→	0·21	19

E. SUMMARY OF MEAN ANNUAL VALES OF Z, i.e. t = 1	Z	%	Z	%
First year from November after settlement	1·16	69	1·36	74
Second year from November to November	3·57	97	3·20	96
Third year from November to November	→	→	0·56	43

APPENDIX III

STATISTICAL EXAMINATION OF RESULTS

It is necessary to test (a) whether the reduction in numbers of each year-class is significant, (b) whether the differences in losses between age groups in the same area are significant and (c) whether the differences in losses recorded outside and inside areas protected by fencing and/or netting are significant.

Gulland (pers. com.) has recommended that a suitable method would be to calculate the instantaneous total mortality coefficients (Z) for each age group from the selected area, and then to determine if each differs significantly (a) from zero, (b) from that of another age group in the same area, and (c) from the same age group in a different area. This calculation is based on the expression

$$N_t = N_0 e^{-Zt} \quad \ldots\ldots\ldots\ldots \text{(Beverton and Holt, 1956)}$$

where N_0, N_t = numbers at beginning and end of time t. The logarithmic transformation of this is $Zt = \log_e N_0 - \log_e N_t$, and the percentage loss represented by each value of Zt may be obtained by reference to the standard e^{-x} tables. The periods of time (t) examined here and in Tables 7 and 8 covered three months (mid-November to mid-February) and two months (mid-November to mid-January), so that equivalent annual values of Z can be obtained by making t equal to $\frac{1}{4}$ and $\frac{1}{6}$ respectively.

In the following example the results obtained in November 1960 and February 1961 (Appendix I) have been examined using the statistical methods of Brownlee (1949). In certain instances, as a result of sampling error, there were apparent increases in the numbers in some samples, which after conversion to logarithms and subtraction resulted in negative values of Zt. Negative values of Zt therefore also occasionally appeared in the calculated confidence limits, and the percentage mortality figures represented by these were obtained by reference to e^x tables.

(a) To test whether the mean mortality coefficient (Zt) differs from zero for each age group treated separately, e.g. inside fenced area (A) – (Table 2)

FIRST-WINTER COCKLES (BROOD)

	Numbers per $\frac{1}{10}$ m² samples 1–10 (Fig. 2)										*Total*
November 1960 (N_0)	513	534	405	576	623	599	550	537	555	568	5,460
February 1961 (N_t)	71	46	297	309	357	86	134	459	416	371	2,546
$Zt = \log_e N_0 - \log_e N_t =$	1·98	2·45	0·31	0·62	0·56	1·94	1·41	0·16	0·29	0·43	0·76

The mean value $\overline{Zt} = 1{\cdot}02$, and is to be compared with the expected value (E) = 0.

$$(\Sigma Zt)^2 = 103{\cdot}02 \qquad \Sigma((Zt)^2) = 16{\cdot}76$$

$$\text{Estimated Variance } (s^2) = \left[\Sigma((Zt)^2) - \frac{(\Sigma Zt)^2}{n}\right] \Big/ n-1$$

$$= \frac{16{\cdot}76 - 10{\cdot}30}{9} = 0{\cdot}72$$

$\therefore$ Estimated Standard deviation $(s) = \sqrt{0{\cdot}72} = 0{\cdot}85$

Standard error of the mean $\overline{Zt} = s/\sqrt{n}$

$$= 0{\cdot}85/\sqrt{10} = 0{\cdot}27$$

* $\text{'t'} = \dfrac{\overline{Zt} - E}{s/\sqrt{n}}$, and since E = 0, $\text{'t'} = \dfrac{1{\cdot}02}{0{\cdot}27}$

$= 3{\cdot}78$ with $n - 1 = 9$ degrees of freedom;

* To avoid confusion, t of Student's test of significance has been denoted 't'.

i.e. the mean mortality coefficient (Zt) is significantly different from zero at the 0·1–1·0% level.

The reduction in the total number of first-winter cockles from 5,460 to 2,546 represents a mortality of 53% (Zt = 0·76).

From calculations of Zt for ten samples, $\overline{Zt}$ = 1·02 (64% loss) with confidence limits at the 95% level of

$$\pm L = \pm s/\sqrt{n} \times \text{'t' (at 9 degrees of freedom)}$$

$$= \pm 0{\cdot}27 \times 2{\cdot}26 = \pm 0{\cdot}61$$

i.e. $\overline{Zt} = 1{\cdot}02 + 0{\cdot}61 = 1{\cdot}63$ (80%)
to $1{\cdot}02 - 0{\cdot}61 = 0{\cdot}41$ (34%)

SECOND-WINTER COCKLES (Table 2)

	Numbers per $\frac{1}{10}$ m², samples 1–10										*Total*
November 1960	104	108	66	115	92	80	53	114	116	58	906
February 1961	4	2	2	7	11	2	2	4	4	16	54
Zt =	3·26	3·99	3·50	2·80	2·12	3·69	3·28	3·35	3·37	1·29	2·82

$\overline{Zt} = 3{\cdot}06$, $(\Sigma Zt)^2 = 939{\cdot}42$, $\Sigma((Zt)^2) = 99{\cdot}75$

$$s = \sqrt{\frac{99{\cdot}75 - 93{\cdot}94}{9}} = 0{\cdot}81$$

Standard error of the mean $= 0{\cdot}80/\sqrt{10} = 0{\cdot}25$

$$\text{'t'} = \frac{3{\cdot}06}{0{\cdot}26} = 12{\cdot}24 \text{ with 9 degrees of freedom;}$$

i.e. highly significant loss at < 0·1% level.

The reduction in the total number of second-winter cockles from 906 to 54 represents a mortality of 94% (Zt = 2·82).

From calculations of Zt for ten samples, $\overline{Zt}$ = 3·07 (95%) with confidence limits at the 95% level of 2·48 (92%) to 3·66 (97%).

COCKLES OLDER THAN SECOND WINTER

Because of the small numbers per sample, and to simplify the mathematics of manipulating logarithms for samples containing no cockles, the ten samples have been grouped in pairs.

	Ten samples of $\frac{1}{10}$ m², grouped in pairs										*Total*
November 1960	(6	2)	(9	10)	(3	7)	(4	10)	(9	4)	64
February 1961	(5	5)	(6	0)	(5	0)	(3	5)	(6	2)	37
Zt =	−0·22		1·15		0·69		0·56		0·49		0·55

Here the negative value of Zt represents an increase in numbers.

$\overline{Zt} = 0{\cdot}53$, $(\Sigma Zt)^2 = 7{\cdot}13$, $\Sigma((Zt)^2) = 2{\cdot}40$

$$s = \sqrt{\frac{2{\cdot}40 - 1{\cdot}43}{4}} = 0{\cdot}49 \quad \frac{s}{\sqrt{n}} = 0{\cdot}22$$

't' = 0·53/0·22 = 2·41 with 4 degrees of freedom.

i.e. significant only at 5–10% level.

The reduction in the total number of cockles older than second winter from 64 to 37 represents a mortality of 42% (Zt = 0·55).

From calculations of Zt from ten samples grouped in five pairs, Zt = 0·53 (41%) with confidence limits at the 5% level of

$$\pm L = \pm 0{\cdot}22 \times 2{\cdot}78 = \pm 0{\cdot}61;$$

i.e. $\overline{Zt} = 0{\cdot}53 + 0{\cdot}61 = 1{\cdot}14$ (68%)
to $0{\cdot}53 - 0{\cdot}61 = -0{\cdot}08$ (−8% = 8% increase).

Negative percentages corresponding to negative values of Zt have been calculated from e^x (not e^{-x}) tables and represent increases in numbers.

From November 1961 to January 1962 (Table 7) the numbers of older cockles were too few for worthwhile analysis in all except netted area (K) and its controls (J + L) in which samples were treated separately, not in pairs as above.

(*b*) *To test whether the differences in mortality coefficients between age groups are significant, e.g. inside fenced area* (*A*).

In this test first- and second-winter values of Zt obtained from the same sample have been compared in pairs to help reduce systematic differences in Zt between sampling positions.

BETWEEN FIRST- AND SECOND-WINTER COCKLES

	Zt values from ten $\frac{1}{10}$ m² samples										*Mean*
First-winter (Zt_A)	1·98	2·45	0·31	0·62	0·56	1·94	1·41	0·16	0·29	0·43	1·02
Second-winter (Zt_B)	3·26	3·99	3·50	2·80	2·12	3·69	3·28	3·35	3·37	1·29	3·06
Difference (Zt_B–Zt_A)	1·28	1·54	3·19	2·18	1·56	1·75	1·87	3·19	3·08	0·86	2·04

The mean value of the difference (Zt_B–Zt_A) is 2·04 and is to be compared with the expected value (E) = 0.

$$(\Sigma Zt)^2 = 420{\cdot}25 \qquad \Sigma((Zt)^2) = 48{\cdot}33$$

$$s^2 = \left[\Sigma((Zt)^2) - \frac{(\Sigma Zt)^2}{n}\right] \Big/ n - 1$$

$$= \frac{48{\cdot}33 - 42{\cdot}02}{9} = \frac{6{\cdot}31}{9} = 0{\cdot}70.$$

.. Standard error of the mean $\overline{Zt} = s/\sqrt{n} = \sqrt{\frac{0{\cdot}70}{10}} = 0{\cdot}26$

't' $= \frac{Zt - E}{s/\sqrt{n}} = \frac{2{\cdot}04}{0{\cdot}26} = 7{\cdot}85$ with 9 degrees of freedom;

i.e. the difference between the mean mortality coefficients for first-winter (Zt_A) and second-winter cockles (Zt_B) is highly significantly different from zero at < 0·1% level.

This method could not be used for a comparison between the mortality coefficients of first- or second-winter with cockles older than second winter, because 1960–1 samples of the latter had already been paired (see previous method). Instead method (*c*) (following) which can be applied to unequal numbers of values of Zt was used, and a highly significant difference was obtained between second-winter and older cockles but not between first-winter and older cockles (Table 7). Method (*b*) was, however, used to compare 1961–2 data (Areas K and J + L – Table 8).

(*c*) *To test whether the differences in mean mortality coefficients of cockles of the same age group between the inside of an area protected by fencing or netting, and its control samples outside, are significant.* The test differs from (*b*) in which results could be paired since they came from the same samples.

Example:

BETWEEN SECOND-WINTER COCKLES FROM NETTED AREA (D) AND ITS CONTROL SAMPLES (C + E) (Table 4)

NETTED AREA (D)

	Numbers per $\frac{1}{10}$ m^2, *samples* 1–5					*Total*
November 1960	97	135	57	111	73	473
February 1961	61	115	50	87	116	429
Zt_A	0·46	0·16	0·13	0·24	(−0·46)	0·10

$\Sigma Zt_A = 0{\cdot}53$, $\overline{Zt}_A = 0{\cdot}11$, $(\Sigma Zt_A)^2 = 0{\cdot}28$, $\Sigma((Zt_A)^2) = 0{\cdot}52$

CONTROL SAMPLES (C + E)

Here logarithmic transformation of zero values has been avoided by calling them unity, then $\log_e 1 = 0$. An alternative method would be to add one to all the values.

	Numbers per $\frac{1}{10}$ m^2, *samples* C(11–15) *and* E(1–5)										*Total*
November 1960	54	36	56	39	119	68	80	58	22	140	672
February 1961	3	6	15	5	4	0	2	2	0	0	37
Zt_B	2·89	1·79	1·32	2·05	3·39	4·22	3·69	3·37	3·09	4·94	2·90

$\Sigma Zt_B = 30{\cdot}75$, $\overline{Zt}_B = 3{\cdot}08$, $(\Sigma Zt_B)^2 = 945{\cdot}56$, $\Sigma((Zt_B)^2) = 105{\cdot}73$

$$s^2 = \frac{\Sigma((Zt_A)^2) - \frac{(\Sigma Zt_A)^2}{n_A} + \Sigma((Zt_B)^2) - \frac{(\Sigma Zt_B)^2}{n_B}}{n_A + n_B - 2}$$

$$= \frac{0{\cdot}52 - \frac{0{\cdot}28}{5} + 105{\cdot}73 - \frac{945{\cdot}56}{10}}{10 + 5 - 2} = 0{\cdot}89;$$

$$s = \sqrt{0{\cdot}89} = 0{\cdot}94$$

$$\text{'t'} = \frac{\overline{Zt}_B - \overline{Zt}_A}{s}\sqrt{\frac{n_A \times n_B}{n_A + n_B}}$$

$$= \frac{3{\cdot}08 - 0{\cdot}11}{0{\cdot}94}\sqrt{\frac{50}{15}} \qquad = 5{\cdot}79 \text{ with 13 degrees of freedom;}$$

i.e. difference is highly significant at $< 0{\cdot}1\%$ level.

Method (*c*) was also used to compare the changes in numbers inside the completely netted area with those in control samples between November 1960 and February 1961, and also in fenced and netted areas and their control samples between November 1961 and January 1962. The results have been shown in Table 7 (November 1960 to February 1961) and Table 8 (November 1961 to January 1962). When comparing the results of the two winters it must be remembered that the period examined statistically in winter 1960–1 covered three months, while that in 1961–2 was two months. This difference has already been adjusted for the data shown in Appendix II.

The variation of Zt amongst samples from the same area, at least among first-winter cockles and among cockles older than second winter (see method (*a*)), is large (as demonstrated by the wide confidence intervals), but nevertheless since the mean values of Zt are significantly different they will be used as a way of estimating and comparing mortalities. It is considered that the wide confidence intervals of Zt, which imply low reliance of data, arise from the fact that samples taken at the beginning and end of time t did not come from

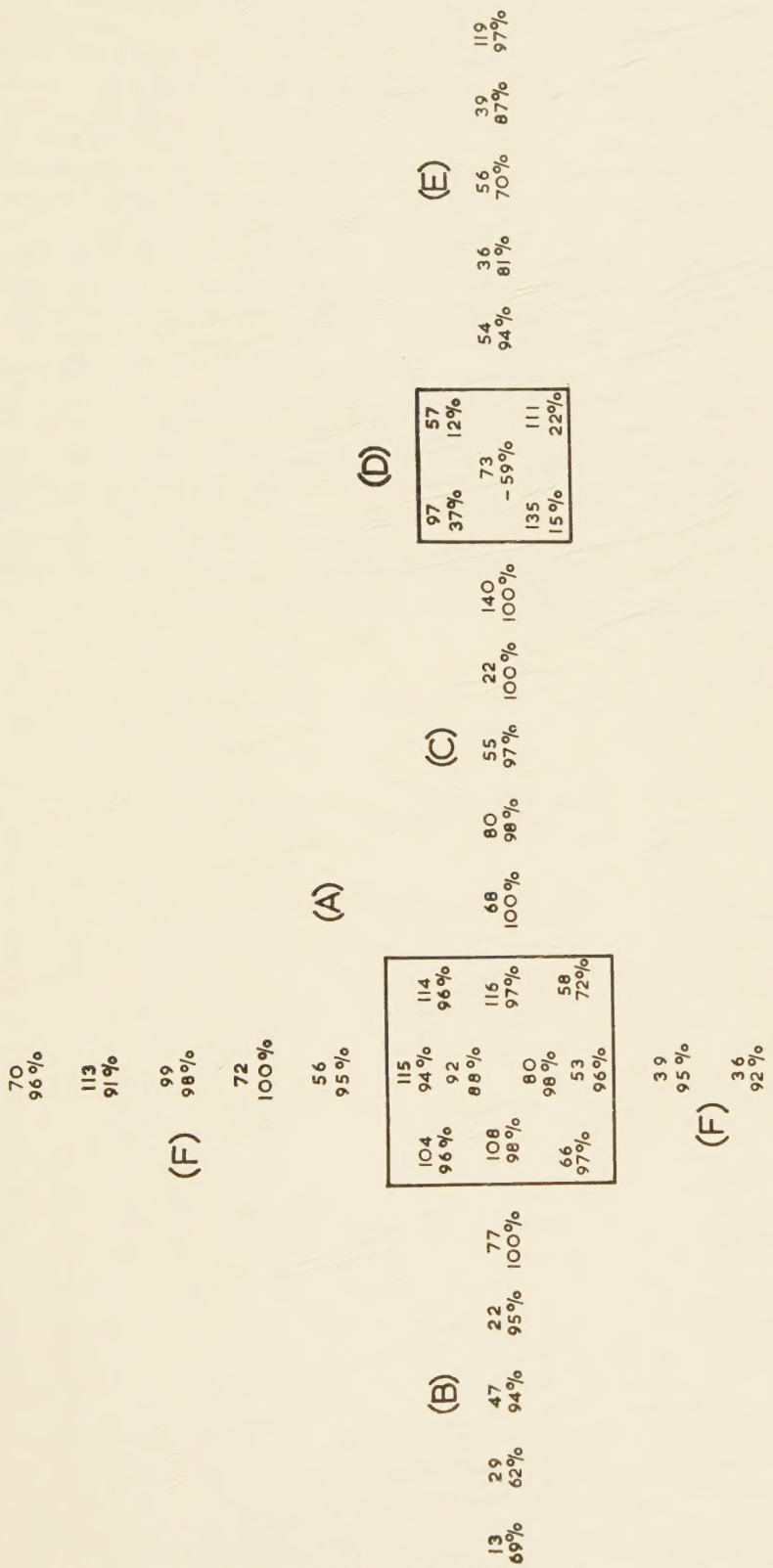

Fig. 7. *Numbers of second-winter cockles in individual* $\frac{1}{10}$*-m*^{2} *samples from sampling areas A to F* (*Figure* 1) *in November* 1960, *together with percentage losses observed between November and February* 1961.

identical positions, and by pairing them in time to estimate mortality per sample the assumption was made that the density was even over the sub-area represented by each sample. This of course was not true (see p. 2 of main text). It would have been possible just to compare the mean numbers in two sets of samples to show the level of mortality – these values of Zt are shown in column 4 of Tables 7 and 8. However this would not have allowed the application of subsequent tests to show the significance of differences between different areas or between different ages. Despite these limitations of the methods, the tests have shown a high level of significance between samples in which the numbers were adequate for analysis.

Tables 7 and 8 confirm the general conclusions reached in the main text, i.e. that mortalities of second-winter cockles were significantly greater than those of either younger or older cockles, both inside and outside areas protected by fencing, but in areas covered by netting the losses showed no significant difference between age groups. It is worth noting that the greatest mortality of older cockles (75%) occurred in control samples (C + E – Table 7), and was believed to have resulted mainly from fishing, but this was still highly significantly less than the mortality of second-winter cockles over the same area. Similarly the greatest winter loss of first-winter cockles of 74% (J + L – Table 8) was highly significantly less than for second-winter cockles. Only in netted area (D) (Table 7) was the mortality of second-winter cockles not significantly more than that of first-winter cockles, while in netted area (K) (Table 8) it was significantly less. The high degree of statistical significance shown in Tables 7 and 8 for the losses of second-winter cockles from areas not protected by netting is demonstrated more clearly in Figure 7, which shows how consistently the high mortality occurred amongst individual $\frac{1}{10}$ m^2 samples.

Table 7. *Statistical analysis of results from experimental areas, November* 1960 *to February* 1961

Index letters in brackets refer to sampling sites in Figure 1. Negative Zt values and percentage mortalities indicate increases in numbers.

Sampling area	Number of samples	Total cockles in November	Zt from totals	% loss of total	$\overline{Zt}$	Mean % loss	% Significance of loss	95% Confidence interval of Zt	95% Confidence interval of % loss	Significance of difference from control
FIRST-WINTER COCKLES										
Fenced area no netting (A)	10	5,460	0·76	53	1·02	64	0·1 →1	0·39 →1·65	32 →80	NO at
Controls (B + C)	10	2,926	0·95	61	1·07	66	<0·1	0·58 →1·56	44 →79	>10%
Netted area (D)	5	357	−0·21	−23	−0·22	−25	>10	−0·70 →0·26	−101 →23	NO at
Controls (C + E)	10	2,818	0·80	55	0·67	49	5→10	−0·03 →1·36	− 3 →74	5 →10%
SECOND-WINTER COCKLES										
(A)	10	906	2·82	94	3·07	95	<0·1	2·48 →3·66	92 →97	NO at
(B + C)	10	556	3·19	96	3·16	96	<0·1	2·24 →4·08	89 →98	>10%
(D)	5	473	0·10	9	0·11	10	>10	−0·32 →0·54	−38 →42	YES at
(C + E)	10	672	2·90	94	3·08	95	<0·1	2·28 →3·87	90 →98	<0·1%
OLDER COCKLES										
(A)	10	64	0·55	42	0·53	41	5 →10	−0·08 →1·14	− 8 →68	NO at
(B + C)	10	59	0·64	47	0·80	55	5 →10	−0·14 →1·73	−15 →82	>10%
(D)	5	24	0·23	21	Not analysed – small numbers					
(C + E)	10	55	1·37	75	1·51	78	1→2	0·44 →2·58	36 →92	

Significance of differences between age groups

	Between first- and second-winter cockles	*Between second-winter and older cockles*	*Between first-winter and older cockles*
Fenced area (no netting) (A)	<0·1%	<0·1%	>10%
Controls (B + C)	0·1 →1%	0·1 →1%	>10%
Netted area (D)	>10%	Small numbers of older cockles	
Controls (C + E)	<0·1%	1 →2%	>10%

Table 8. *Statistical analysis of results from experimental areas, November 1961 to January 1962*

Index letters in brackets refer to sampling sites in Figure 1. Negative Zt values and percentage mortalities indicate increases in numbers.

Sampling area	Number of samples	Total cockles in November	Zt from totals	% loss of total	$\bar{Z}t$	Mean % loss	% Significance of loss	95% Confidence interval of Zt	95% Confidence interval of % loss	Significance of difference from control
FIRST-WINTER COCKLES										
Fenced area no netting (A)	10	2,011	0·99	63	0·90	59	<0·1	0·54 →1·26	42 →72	NO at
Controls (B + C)	9	2,654	0·68	49	0·72	51	2 →5	0·05 →1·39	5 →75	>10%
Netted area (K)	8	944	0·53	41	0·52	41	2 →5	0·09 →0·95	9 →61	YES at
Controls (J + L)	10	1,701	1·33	74	1·47	77	<0·1	1·04 →1·91	65 →85	0·1 →1%
Netted area open sides (H)	8	1,278	0·35	30	0·34	28	1 →2	0·07 →0·60	7 →45	YES at
Controls (G + J)	10	2,718	0·82	56	0·96	62	<0·1	0·61 →1·31	46 →73	<0·1%
SECOND-WINTER COCKLES										
(A)	10	1,383	3·04	95	3·11	95	<0·1	2·10 →4·11	88 →98	NO at
(B + C)*	5	707	4·16	98	4·25	98	<0·1	3·35 →5·15	97 →99	>10%
	4	51	0·15	14	—	—	—	—	—	
(K)	8	1,147	0·03	3	0·05	5	>10	−0·06 →0·16	− 6 →15	YES at
(J + L)	10	1,618	2·36	91	2·41	91	<0·1	1·14 →3·69	68 →97	<0·1%
(H)	8	1,457	0·46	37	0·49	39	1 →2	0·11 →0·87	11 →58	YES at
(G + J)	10	1,589	2·64	93	2·88	94	<0·1	2·17 →3·59	89 →97	<0·1%
OLDER COCKLES										
(A)	10	28	−0·33	−39	—	—	—	—	—	—
(B + C)	9	33	0·35	30	—	—	—	—	—	—
(K)	8	56	−0·39	−48	−0·35	−42	>10	−1·10 →0·40	−200 →33	YES at
(J + L)	10	81	0·41	33	0·54	42	1 →2	0·16 →0·92	15 →60	<0·1%
(H)	8	39	−0·12	−13	—	—	—	—	—	—
(G + J)	10	38	0·27	24	—	—	—	—	—	—

* Control samples B and C have been analysed separately to reduce the effects of bias caused by small numbers in samples B.
— Numbers too small for worthwhile analysis.

Significance of difference between age groups

	Between first- and second-winter cockles	*Between second-winter and older cockles*	*Between first-winter and older cockles*
Fenced area (no netting) (A)	<0·1%	—	—
Controls (B + C)	1 →2%	—	—
Netted area (K)	2–5%	>10%	5 →10%
Controls (J + L)	<0·1%	<0·1%	0·1 →1%
Netted area, open sides (H)	>10%	—	—
Controls (G + J)	<0·1%	—	—

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